

# MONOGRAPH ON THE GENETICS OF PHASEOLUS

BY

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MONOGRAPH ON THE GENETICS OF PHASEOLUS  
(especially *Ph. vulgaris* and *Ph. multiflorus*)

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## I. INTRODUCTION

As beans form an extremely important agricultural and horticultural crop plant all over the world, the existence of an extensive literature on the subject is only natural. This holds also good with respect to the genetical investigation of several characters, partly of theoretical, partly of merely practical interest. In some respects these investigations have given valuable and conclusive results. From the present paper it will, I hope, become apparent that there is considerable confusion, to solve which it will require much further investigation.

On several occasions part of this literature has been more or less thoroughly summarised as an introduction to new data reported. Especially a paper by TEN DOORNKAAT-KOOLMAN (18, 1927) should be mentioned. A review is also found in FRUWIRTH's *Handbuch der landwirtschaftlichen Pflanzenzüchtung*, Vol. 3. The present reviewer (57, 1923) has also given a summary of the principal data, that is, however, especially adopted to the needs of seedsmen, without reference to literature. I also make mention of the work of MATSUURA (72, 1929), genus *Phaseolus*, though it is incomplete and not free from errors.

The genus *Phaseolus* is cosmopolitan. The species *Ph. vulgaris* and *multiflorus* (*coccineus*), with which we will have to deal nearly exclusively, are now generally considered to be South-American. The former, however, is not known in a wild state. Moreover, as it belongs to the oldest cultivated plants, which in prehistoric times must have been distributed all over the world, we cannot be absolutely sure of its native country. The problem has been dealt with by IVANOV (43, 1928), according to the principles of VAVILOV, in a paper that forms a part of the admirable work of the latter together with his collaborators. Principally it is based on geographical distribution of races, morphological comparison and immunity against diseases. From the data obtained it is concluded that *Ph. vulgaris*, *lunatus*, *multiflorus*, *acutifolius* and *caracalla* are of American origin, *Ph. aureus*, *Mungo*, *aconitifolius* and *calcaratus* are native of Southwestern Asia, *Ph. angularis* of Southeastern Asia.

As with most other cultivated forms, it is improbable that a reliable conception can ever be formed of the way in which the poly-

morphy of the species *vulgaris* came into being. Hybridisation, no doubt, will have played a part. The species conception in such a case is the superlative of subjective and the splitting up of the *vulgaris*-group into smaller systematic unities has quite a history, which may be traced by the study of a fair number of publications. As many of these contain, besides a systematic division, useful descriptions and indications of synonymy of the locally different racial denominations, both historical and practical interest are served by an enumeration of the principal papers. I mention SAVI (86, 1822), FINGERHUTH (29, 1835), MARTENS (71, 1860), IRISH (42, 1901), DENAFFE (16, 1906), TRACY (118, 1907), JARVIS (44, 1908), COMES (10, 1909), WITTMACK (136, 1922), BECKER-DILLINGEN (3, 1929). Also TEN DOORNKAAT-KOOLMAN (18, 1927) considers the problem of a scientific and at the same time practical system.

Considering the *vulgaris*-group to be a species, to my knowledge only one interspecific hybrid is reported: *Ph. vulgaris*  $\times$  *multiflorus* and rec. Other crosses (at least with *Ph. lunatus*) have been tried, but failed.

The chromosome number has been investigated by several experimenters. Of these KLEINMANN (55, 1923) for *Ph. multiflorus* and RAU (82, 1929) for *Ph. Mungo* and *radiatus* came to the haploid number = 12 resp.  $2n = 24$ . KARPECHENKO (52, 1924) observed a diploid number of 22 in all species investigated (*Ph. vulgaris*, *multiflorus*, *lunatus*, *Mungo*, *acutifolius*, *aureus*, *angularis*, *trilobus*). The same number was found by WEINSTEIN (134, 1926) for *Ph. vulgaris*, by MUTO (76, 1929) for *Ph. chrysanthos*, by KATAYAMA (53, 1928) for *Phaseolus radiatus* and by KUHN (61, 1929) for *Ph. multiflorus* and *vulgaris*.

Further KARPECHENKO's investigation of the species hybrid *Ph. vulgaris*  $\times$  *multiflorus* "reveals normal spindles in the heterotypic and homoeotypic mitosis, the chromosomes forming normal equatorial plates, though not unfrequently one or two of them lie apart from the others."

### Biology

The bean flower is of a rather complicate structure, which it is necessary to understand in connection with the occurrence of spontaneous hybrids as well as the technique of the production of artificial

hybrids. According to DARWIN the flower has been described by DEL PINO and also by FARRER (25, 1868). FRANCIS DARWIN (15, 1874) described a small vertical projection on the single free stamen which prevents insects to reach the nectar unless entering the flowers from the left wing petal. DARWIN (14a, 0000; 2nd ed. 1900, p. 150. See also 14, 1858) says of *Ph. multiflorus* "The flowers are so constructed that hive- and humblebees, which visit them incessantly, almost always arrive on the left wing-petal, as they can best suck the nectar from this side. Their weight and movements depress the petal, and this causes the stigma to protrude from the spirally-wound keel, and a brush of hair round the stigma pushes out the pollen before it". See also HERMANN MÜLLER (75a, 1873) and TSCHERMAK (120, 1901).

This does not only hold true for *Ph. multiflorus*, which is to be regarded as preferentially cross-fertilising, but equally for *Ph. vulgaris*, which is a fully selffertile species. Of the latter a figure is here given, from which the mechanism may be understood as follows: The weight of the visiting insect presses down the left wing, which, according to TSCHERMAK (1901) articulates with the keel slightly above the basis. The keelbasis is compressed, which causes a shifting of the keel and protrusion of the stigma.

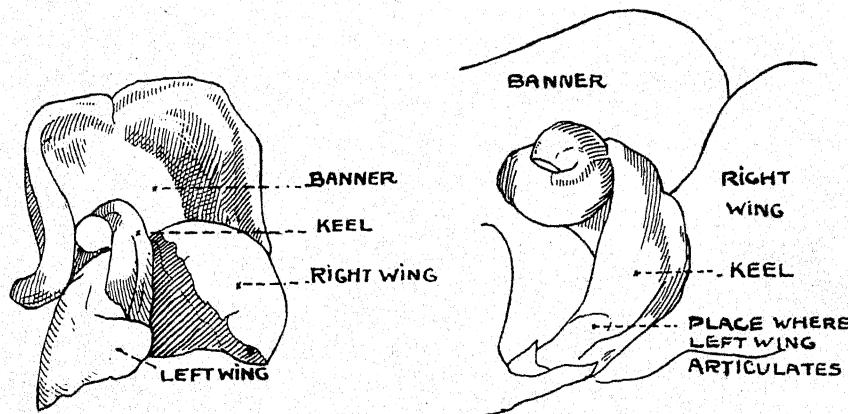


FIG. 1.

As to the insects which in Europe visit bean flowers, DARWIN mentions hive- and humble-bees, FRUWIRTH *Megachile maritima* K., *Osmia maritima* FRIESE, *Deilephila galii* ROT., *Chariclea umbra* HFN.,

*Bombus hortorum* L. and *B. terrestre*, LENZ hive- and humble-bees, flies and butterflies.

DARWIN (14a, 1900, p. 433), SCHRÖDER (1901), LENZ (63, 1920) a.o. observed that *B. terrestris* and the hive-bee perforate the flowers at the base to get at the nectar. That this is not always the case is well known. DARWIN says "I .. daily saw humble- and hive-bees sucking at the mouths of the flowers. But one day I found several humble-bees employed in cutting holes in flower after flower; and on the next day every single hive-bee .... sucked through the holes .... made by the humble-bees".

Which animals in tropical America are the cross-fertilisers I do not know. BELT (4, 1874, cited after DARWIN) relates that *Ph. multiflorus*, though flowering well in Nicaragua did not produce a single pod as the native bees did not visit the flowers. Similar cases, observed by DODEL and LINDMANN, are reported by v. KIRCHNER (54, 1905). The suggestion, made by LENZ (64, 1921) that the natural cross-fertilisers might be colibries seems mere guess-work.

The statement that *Ph. multiflorus* is a preferential cross-fertiliser implies that omission of cross-fertilisation (or perhaps of artificial self-fertilisation) should result in diminished seed production. The reports on this point, however, differ.

DARWIN (14a, 1900) isolated some plants under a net and found that these plants developed from  $\frac{1}{3}$  to  $\frac{1}{8}$  of the number of pods, which unprotected plants produced. SIRKS (100/101, 1922) also observed largely diminished seed production on isolated plants. OGLE (79, 1870) and v. TSCHERMAK (121, 1902) did not get a single pod from isolated plants. FRUWIRTH (32, p. 193) repeatedly tried to obtain seed from isolated plants. In some cases he got no seed at all, in other cases normal seed production. This seems to point to different behaviour of different races or individuals. To the same conclusion points a statement of TJEBBES (112, 1925), that he was able to select pure lines with a satisfactory degree of self-fertility when artificially selfed. Among the offspring of varietal hybrids he further found individuals which were apparently to a high degree self-sterile, other ones being relatively self-fertile. (Cf. also p. 386). Whether the observed self-sterility in most cases is physiological or mechanical is not known. DARWIN states (14a, 1900, p. 152) that he obtained self-fertilised seeds by moving up and down, in the same manner as bees

do, the wing-petals of the flowers. FRUWIRTH (32, 1924) however found no difference in the number of pods between plants treated in this way and untouched ones, and TSCHERMAK (120, 1901 p. 703) states that this procedure does not result in self-pollination.

*Phaseolus vulgaris* is entirely self-fertile, and self-fertilisation is by many considered to be the rule. This is furthered by an early shedding of the pollen directly on the stigma, the anthers opening already before the flower opens. Yet spontaneous hybridisation is by no means rare. HOFFMANN (39, 1874) doubtless had to do with spontaneous hybrids, but as in no case he could raise artificial hybrids, he attributed the mixed character of the seed to spontaneous variability. DARWIN (14a, 1900, p. 153) says that varieties grown near one another sometimes cross largely and reports on some cases (14, 1858). Equally to GÄRTNER (33, 1849) and FOCKE (30, 1881) the occurrence was well-known.

EMERSON (20, 1904) observed from 1—10 % of spontaneous hybrids and (21, 1909) reports on investigations, carried out with the purpose to state the frequency of hybridisation. Among the offspring of 100 races grown near one another he observed 4 % hybrids. MAYER GMELIN (73, 1916) especially investigated the percentage of spontaneous hybrids. He found figures ranging from 1.02—3.65 %.

LENZ (63, 1920) found among bush-beans Hinrichs Riesen, cultivated the year before side by side with Zeppelin pole-beans, 1.3 % of hybrids. SCHIEMANN (93, 1920) observed in material from different sources, cultivated in Potsdam, spontaneous hybridisation between *vulgaris* races in from 0.78—2.78 %; in pure lines 1917: 2.11 %, 1918 0.79 %, 1919: 0.93 %. KRISTOFFERSON (59, 1921) has tested a large number of varieties and observed from 0—12.99 % with an average of 0.83 % for 1918, of 1.15 % for 1919. Of course the frequency of cross-fertilisation between flowers of the same plant and of such between plants belonging to the same line or race must be much greater, as has been stated by many authors. The percentage of cross-fertilisation is moreover diminished by the fact that in most cases the optima of the flowering periods of different races will not coincide. LENZ (64, 1921) is even of the opinion that a figure as large as about 75 % of cross-fertilisation is not impossible, though not probable. On the other hand local as well as racial differences may be of much importance. The matter is of the greatest importance with respect to the in-

vestigations of JOHANNSEN, who regarded the bush-bean as almost exclusively self-fertilising (cf. SCHIEMANN 93, 1920; LENZ 63, 64, 1920/21). Spontaneous hybridisation between *Ph. vulgaris* and *Ph. multiflorus* has also repeatedly been reported, *vulgaris* always being indicated as the seed parent (KÖRNICKE 58, 1876; DE VRIES 17, '01s—'03; 1903; MAYER GMELIN 73, 1916; LENZ 63, 1920; SCHIEMANN 93, 1920). Probably also DANIEL (13, 1900).

The  $F_1$  hybrid between *Ph. vulgaris* and *multiflorus* is by most experimenters stated to be of a considerably diminished fertility, whereas in  $F_2$  and further generations different degrees of fertility, even up to apparently normal (TSCHERMAK 122, 1904), occur.

MENDEL (74, 1865) says of the  $F_1$  hybrids "Their fertility was very limited" and of the second generation: "No plant could rank as fully fertile; many produced no fruit at all; others only yielded fruits from the flowers last produced, which did not ripen .... The greatest disposition to infertility was seen in the forms with preponderantly red flowers". From further generations Mendel concluded that even among the offspring of fairly fertile plants there came again some which were less fertile or even quite sterile.

TSCHERMAK (120, 1901; 121, 1902) describes the  $F_1$  plants as late. When plants were early sown in the glass house and later on planted out in the open, the seed production was rather satisfactory (348 seeds from 4 plants, against 79 seeds from 6 plants, sown directly in the open). This proves that the observed infertility is partly a consequence of lateness. Among  $F_2$  and further generation plants the fertility was different, some being sterile, others slightly to nearly fully fertile. Artificial self-pollination in most cases failed. The author could not confirm Mendel's observation that red flower-colour is more or less associated with sterility.

KARPECHENKO (52, 1925) simply speaks of the hybrids as almost sterile.

TJEBBES (112, 1927) found all giant  $F_1$  plants to be quite sterile. Part of the  $F_1$  dwarfs of normal character produced some seeds. Also in the  $F_2$  generation many plants were of diminished fertility or quite sterile.

TEN DOORNAAT-KOOLMAN (18, 1927) could not, for his crosses, confirm the sterility of the  $F_1$  hybrids. His normal twining  $F_1$  types were vigorous plants, which flowered and fruited abundantly, but

ripened their seeds too late. In further generations he found an often diminished fertility, mainly correlated with either too luxuriant growth or dwarfing. In an unguarded  $F_2$ , among 111 flowering plants, 92 fruited and of these 3 produced only empty fruits. Isolation of  $F_2$  and  $F_3$  plants compared with insect-fertilisation of the same plants permitted to distinguish the following groups:

1. Rather fertile when isolated as well as when unguarded.
2. Infertile when isolated, yet forming small pods, that wither in a young stage of development. When unguarded, in exceptional cases a single one-seeded pod developed.
3. Infertile when isolated as well as when unguarded.
4. Infertile when isolated, fertile when unguarded.

The number of plants belonging to group 1, 2 + 3 and 4 were respectively 9, 8 and 14.

If we reconsider the matter of pollination and fertility for both species and their hybrid, the relations appear to be not at all solved. The following statement might be given as a working hypothesis:

1. *Ph. vulgaris*, fully self-fertile.
2. *Ph. multiflorus*
  - a. self-fertilising when simply isolated.
  - b. self-fertile when artificially pollinated.
  - c. to a certain degree or even fully self-sterile, yet fertile when cross-fertilized.
3. *Ph. vulgaris*  $\times$  *multiflorus* and reciprocal.

$F_1$  self-fertile to entirely sterile.

Offspring:

- a. self-fertilising when simply isolated.
- b. fertile after artificial self-pollination.
- c. self-sterile, cross-fertile.
- d. sterile (female sterility).

Further the pollen-sterility should be considered.

TSCHERMAK (123, 1912) and TEN DOORNKAAT-KOOLMAN (18, 1927) state that red flower colour is correlated with a tendency to cross-fertilisation. The latter observed that both the *vulgaris*- and the *multiflorus* flower type may be either self-fertile or self-sterile. As the self-sterility and self-fertility in beans seems partly to be due to the relative position of anthers and stigma, this point should also be considered in connection with the statement given above.

TEN DOORNKAAT-KOOLMAN further considers the problem of sterility in the light of a lethal factor hypothesis. (p. 170).

### *Technique in hybridization*

As both *Ph. multiflorus* and *Ph. vulgaris* shed their pollen before the opening of the flowers, measures should be taken in time to guard the stigma of flowers to be cross-fertilised against their own pollen. This should be done as soon as the bud is nearly full-grown, but before the banner petal begins to open.

Emasculation is the safest procedure, but it is very difficult on account of the spirally wound keel. The danger is great to injure the style, which is fatal. TSCHERMAK (120, 1901) and EMERSON (19, 1902) describe the procedure.

v. TSCHERMAK (120, 1901) describes a method that in practice is very satisfactory. The left wing petal of the full-grown bud is, as insects do when visiting the flower, pressed down, which causes the stigma to protrude. If the pressure is strong enough the keel basis is injured and the stigma does not reenter.

In both cases pollination with the race chosen as a pollen parent can at once be performed, as the stigma is usually receptive. This can best be done by taking a mature flower of which the stigma is caused to protrude. The brush of hairs round the stigma will be covered with pollen, which is lightly rubbed against the stigma of the flower to be fertilised. After pollination the flower, better still the whole plant should be guarded against insects by means of a cloth cover until the fruit has set.  $F_1$  and further generation plants should equally be protected against insects.

Varietal hybrids within the species *Ph. vulgaris* will show full fertility when thus isolated. In order to self-fertilise hybrids between *Ph. multiflorus* races as well as *Ph. vulgaris*  $\times$  *multiflorus* it might be advisable to press the left wing petals of mature flowers as was practised by DARWIN.

### *Graftage*

Different forms of *Ph. vulgaris* may be easily united by graftage (FRUWIRTH 32, 1924, p. 191). DANIEL (12, 1897 and other papers)

supposes to have observed graft hybrids. TJEBBES and KOOIMAN (114, 1919) practised this technique in order to investigate the genetics of albino seedlings. Equally the union of different species, *Ph. vulgaris* and *Ph. multiflorus* is possible. RICHMOND (84 1926) united *Ph. vulgaris* and *lunatus* by a process known as inarching, a method of side-grafting in which both stock and scion are attached to their own roots until the parts are united. The influence of stock and scion was here of a most curious kind. When *Ph. lunatus* was grafted upon *Ph. vulgaris* the plant was not able to grow root nodules when inoculated with bacteria taken from *lunatus* root nodules. Yet the growths was stimulated and atmospheric nitrogen assimilated. Mutatis mutandus the same holds true for *Ph. vulgaris* grafted upon *Ph. lunatus*. The seeds borne by such plants, however were able to form root nodules with the bacteria, characteristic for the stock, whereas in controls bacteria and beans proved not to have been able to adapt themselves to each other.

#### *Bud sports. Vegetative segregation. Mutation*

JOHANNSEN (47, 1909) describes two bud sports in his pure lines. Of these one has been mentioned under the heading Albinism and variegation, p. 307. A second one was a narrow-leaved branch, that however did not produce a single seed.

REINKE (83, 1915) describes a white-flowered sectorial sport of *Ph. multiflorus*. This case is further referred to on p. 383.

TSCHERMAK (125/126, 1919) observed a most interesting case of vegetative segregation in a  $F_8$  combined hybrid *Phaseolus multiflorus* (White Russian Giant)  $\times$  (*Phaseolus multifl. coccineus*  $\times$  *Ph. vulg.* "Wachsdattel) red-flowered, black-seeded. Of this plant three pods were harvested. Two of these pods contained the expected black seeds, the third however contained two nearly white seeds with a curious greyish violet pattern. The black seeds of this plant produced:

- 1 white-flowered, white seeded
- 2 red-flowered, black-seeded.

The white seeds with violet pattern did not breed true, neither were bud sports produced. One produced a red-flowered black-seeded plant, the other a red-flowered, brown-seeded one. Another case, comparable to the one cited above, was observed in a hybrid between

the races Refuge and Hinrich's Riesen. It is not described, only given in an imperfect photographic reproduction. Apparently a plant with dark self-coloured seeds has given a sport with striped seeds. The case might have presented considerable interest; about the offspring, however, nothing has been related.

JOHANNSEN (48, 1911) also describes mutations with respect to seed-dimensions. One of these "mutants" proved to be constant, another one segregated into 1 original type: 2 heterozygous: 1 broad type (the "mutant"). Another case is reported by SCHIEMANN (93, 1920).

An abnormal plant, "unifoliolata" has been described as a mutant of *Ph. multiflorus* by RIESER (85, 1926). As it had abnormal flowers it has produced no offspring.

Here a most interesting case of an attempt to modify the germ plasm by HOFMANN (41, 1927) may be considered. This experimenter subjected seeds and growing plants of the Navy bean to a treatment with a 0.75 % solution of chloral hydrate which caused several modifications, dwarfing, diseased appearance, much like that found in plants infected with virus diseases, asymmetrical leaf development. The offspring of such treated plants were to a large percentage (75 %) aberrant types which persisted through six generations. These must be considered as non hereditary ("Dauermodifikationen"). In subsequent generations the percentage of aberrant types diminished; the hybrids of normal plants ♀ × aberrant types ♂ are normal and back-crosses of these hybrids with aberrant types as pollen parents do not produce any aberrant types. Consequently the modification is only transmitted by the eggcells, not by their chromatine, but by their gradually recovering cytoplasm.

DANIEL (12, 13, 13a, 13b) reports to have observed hereditary alterations by means of mixed grafting. Haricot de Soissons Gros was used as stock, Haricot Noir de Belgique as scion. The author found that the tender structure of the pod and the agreeable taste of the scion have been hereditarily altered, though the offspring differed less from the pure race than did the scion. In the second generation however various types occurred that prove to anyone not prejudiced that the scion must have been cross-fertilized by *Ph. multiflorus*. In other respects DANIEL's conclusions appear to be equally lacking critical foundation. GRIFFON (34a, 1913) repeated DANIEL's experiments with negative results.

*Heterosis*

In a monograph like the present a discussion of a general problem like that of heterosis is not desirable. It may be simply stated here that such a discussion in connection with heterosis in bean hybrids is to be found in TEN DOORNKAAT-KOOLMANS' theses. The phenomenal growth of some hybrids between *Ph. vulgaris* and *multiflorus* is apparently to be considered as a consequence of a heterosis stimulation. It is considered in connection with sterility and lateness.

Heterosis not connected with sterility is described by MALINOWSKI (69, 1924; 70, 1928). In this case lateness in ripening is also observed. He states that in  $F_2$  and further generations equally prosperous plants are segregated, which points to the conclusion, that the heterosis is merely the consequence of a favourable combination of mendelian factors. The same author (68, 1921) also describes a case of heterosis with respect to seed dimensions. ("Disjonction transgressive non-symétrique — un cas particulier de "Heterosis"). Whether for such cases the term heterosis (which implies a more or less mysterious stimulation on account of the heterozygous condition) should be applied seems doubtful.

## II. PLANT COLOUR

The colour of the bean plant as a whole may be normally of a lighter or darker green. The green colour, moreover, may be tinged with violet, as in the variety Blue Pod Butter. The interrelation of the general plant colour and other characters has not been purposely studied. Yet such relations doubtless exist. Thus white-seeded, white-flowered varieties of *Ph. multiflorus* have the foliage much lighter coloured than red-flowered forms. Further in the variety Blue Pod Butter the buff colour of the seeds, the dark coloured flowers and the purplish tinge of the whole plant, especially of the pods, are so closely associated that this combination is segregated from hybrids of Blue Pod Butter with other races as a unity (SHAW and NORTON 95, 1918). As abnormal general colours we may consider *aurea*, white and variegated.

*Aurea*

JOHANNSEN (47, 1909) observed 2 aurea plants among 6000 off-

spring in one of his pure lines. He has only proved their constancy and made no crosses with normal green plants. He supposed that one of his pure line plants may have produced an *aurea* bud-sport.

### *Albinism and variegation*

Albinism and variegation, though common enough in the vegetable kingdom, have for beans only been reported in a couple of cases.

JOHANNSEN (47, 1909) found albinism as a bud sport (termed by him Knospenmutation) in one of his pure lines. On a purely white branch one pod with four seeds developed. These seeds had normal seed coat colour and gave rise to pure albino plants that perished when quite young.

Sometimes, as observed by TJEBBES and KOOIMAN (114, 1919) in a culture of citroenboonen (bean with a lemon-coloured seed coat) regularly a small percentage of the seedlings are albinotic and die in an early stage of development. Of three normal plants isolated only one proved to be heterozygous and produced 26 green seedlings and 8 yellow ones. Of the albino seedlings some were grafted upon normal green plants. They then proved to be no real albinos but developed a small number of minute patches of pale green on the leaves and narrow stripes on the pods. The number of seeds produced in this way by two variegated plants was only 5. They gave variegated plants exactly like the mother plant. The albinotic strain is supposed to have arisen either from spontaneous cross-fertilisation between a normal green plant and an albino (or variegated) bud-sport, or from the loss of a chlorophyll factor in one single flower.

The development of the small patches of chlorophyll is an unsolved problem. Either the plants must be considered as an extreme case of variegation or the albino scion must have received some chemical substance from the stock, thus enabling the development of chlorophyll.

### *Stem colour*

The colour of the stem may be either green or tinged with pink or red. They are best distinguished in the hypocotyls. A certain relation between stem colour and flower colour is stated by MIYAKE a.o.

(75, 1930). Red stem colour is accompanied by red flower, pink stem by pink flower, whereas green stem colour occurs with all flower colours (red, pink, flecked and white). A factorial representation is not given. The crosses are following:

Red  $\times$  pink,  $F_1$  red,  $F_2$  3 red : 1 green.  
Pink  $\times$  green,  $F_1$  red,  $F_2$  9 red : 3 pink : 4 green.  
Red  $\times$  green,  $F_1$  red,  $F_2$  3 red : 1 green.  
id.  $F_1$  red,  $F_2$  9 red : 3 pink : 4 green.  
Green  $\times$  green  $F_1$  red,  $F_2$  9 red : 7 green.

Cf. also page 320.

The chlorophyll characters of the pod are treated in relation with other colour characters of the same organ (p. 325), equally those of the seeds (p. 332).

### III. PLANT HEIGHT AND HABIT

#### *Phaseolus vulgaris*

In beans two main types of habit may be distinguished: short, erect, non-twining (bush beans) and long, twining (pole beans). The first type has botanically been distinguished as a separate species, *Ph. nanus*. Besides there is a more or less intermediate type, commonly classed with bush beans, but better classed runner beans, characterized by indeterminate(?) growth, few but rather long internodes and a tendency to twining (Fädeln). FRUWIRTH (32, 1924, p. 179) observed such runner types among ordinary bush beans. The type proved to breed true and dominates over the ordinary bush bean type. FRUWIRTH considered these runners to be mutants. He further states that such runners are rather frequently observed; also that the character often occurs as a modification under favorable circumstances. Apparently the matter may be put in words as follows: In many varieties the tendency to form runners is a racial character, that is in some cases easily realized, in other races requires more favorable conditions.

v. TSCHERMAK (122, 1904; 123, 1912) gives some data that do not agree with the observations by other experimenters. In crosses of bush with tall twining types,  $F_1$  was somewhat shorter than the tall parent.

$F_2$  was classed as follows: 45 tall, 11 intermediate, 28 bush. Both tall and bush types segregated into the same three classes. The bush types gave tall and intermediate types in small numbers only. To explain these facts TSCHERMAK thinks at least two factors necessary. As EMERSON (24, 1916) makes probable this representation of the facts may be a consequence of the circumstance that TSCHERMAK did not analyse the nature of the differences between height and habit types.

EMERSON (20, 1904; 24, 1916) gives a thorough analysis of the problem. He states that the differences in height between bean races have at least three causes:

1. In bush beans the growth is determinate; that is, after a small number of internodes (usually 4—8) have developed, the axis terminates in an inflorescence. In pole beans the inflorescences develop in the leaf axils, the number of internodes being indeterminate, varying to a large extent with external conditions. EMERSON studied the behaviour of this set of characters in 948  $F_1$  plants of crosses between pole and bush beans of a great many distinct races; all these  $F_1$  plants had indeterminate growth. Of 1104  $F_2$ -plants 832 were indeterminate, 272 determinate, showing a clear cut 3 : 1 segregation.

2. The number of internodes in pole beans depends largely on external conditions. Under given conditions the number of internodes will however have for any distinct race a characteristic value. In bush beans the number of internodes is small and little influenced by external conditions. In such a bush bean a tendency to develop a high internode number may however be suppressed by the determinate growth. The following table gives a summary of some of EMERSON's results of crosses between Red Marrow (tall bush), Triumph (short bush), July (tall pole bean) and Snowflake (short pole bean).

Race or Cross	Mean of P	Mean of F <sub>1</sub>	Mean of F <sub>2</sub> pole-bean segregates	Mean of F <sub>2</sub> bush segregates
Red Marrow . .	5.78 $\pm$ 0.05			
Triumph . . .	5.98 $\pm$ 0.04			
Snowflake . . .	20.48 $\pm$ 0.44			
July . . . . .	27.82 $\pm$ 0.55			
Red Marrow × Snowflake		26.56 $\pm$ 0.48	26.31 $\pm$ 0.47	5.45 $\pm$ 0.16
Red Marrow × July . . .		26.00 $\pm$ 0.74	?	6.13 $\pm$ 0.14
Triumph × Snowflake . .		31.36 $\pm$ 0.59	23.32 $\pm$ 0.54	5.69 $\pm$ 0.13
Triumph × July		?	?	5.90 $\pm$ 0.11

The high internode number of F<sub>1</sub> Triumph × Snowflake is according to EMERSON probably due to the vigor of growth and lateness induced by heterosis. An indication of segregation of factors for number of internodes is seen in the cross Red Marrow × Snowflake. The coefficient of variations for Red Marrow is 10.76  $\pm$  0.57 %, that of the F<sub>2</sub> bush-bean segregates being 19.65  $\pm$  2.18 %. Segregation is also shown in F<sub>4</sub> of Longfellow × Fillbasket where two lines have been selected having means of 7.44 and 5.17 internodes respectively.

3. Internode length is greater in the shortest pole bean than in the longest bush bean. EMERSON shows however that the length of bush internodes is influenced by the early termination of the main axis and points out that the only method for accurately testing the potential internode length of bush beans is to cross them with pole beans and compare the internode length of F<sub>2</sub> offspring with that of the pole-bean parent. It would carry us too far if we considered this in details.

In this analysis EMERSON does not consider the twining habit, as he seems to have provisionally done in an earlier publication (22a, 1910, cited after NORTON 78, 1915).

Actually NORTON, in an analysis that to some extent covers that

by EMERSON, considers the twining habit as a distinct quality. Like EMERSON he opposes determinate to indeterminate growth and supposes a series of polymerous factors for length of axis. He does not consider the actual internode number as EMERSON did, but discerns between twining and non-twining habit. In a simple factorial way the possible combinations may be thus represented:

A—a : indeterminate versus determinate growth

L—l : tall vs short axis

T—t : twining vs non-twining habit.

ALT pole beans

ALT runner beans (non twining pole beans).

ALT shoots (main axis short, some few early, twining shoots).

Alt semi runners

aLT and aLt, spreading forms with long outstretched branches  
aLT and alt, erect, bush bean.

From the foregoing it may be safely stated that the main difference between bush and pole beans is caused by the characters determinate vs indeterminate growth. Minor factors may influence the main types.

Simple 3 : 1 segregation has also been observed by MCROSTIE (67, 1919) and TJEBBES and KOOIMAN (115, 1921). TEN DOORNKAAT-KOOLMAN (18, 1927) found in a number of crosses 1013 pole beans : 292 bush beans, which equally points to a simple 3 : 1 segregation. The excess of pole beans may be partly connected with the appearance of bush beans with a tendency to twining.

SURFACE (105, 1916) observed a relation of eye pattern of the seed coat and type of vine. He states that with few exceptions all Old-fashioned Yellow Eye pure lines had the bush type of vine, nearly all lines of Improved Yellow Eye short runner type. These runner beans are described as "of the short runner or short pole type, rarely reaching a total height of more than 125 centimeters" showing axillary inflorescences and twining habit. "Under ordinary conditions such beans do not show indeterminate growth", according to Surface, because the growth is stopped early by unfavourable conditions. The data of hybrids between both eyed types (the vine type of the parental lines and  $F_1$  hybrids are not recorded) are taken from  $F_2$ — $F_n$

generations. Piebald is the heterozygous type between both eye types mentioned (see p. 380). Among piebald we find 70 runners : 54 bush; among Improved Yellow Eye type 24 runners : 19 bush; among Old-fashioned Eye type no runners : 58 bush. These figures cannot be interpreted on account of the too scanty information. The only interesting fact is the total absence of runners among Old-fashioned Eye type. This fact is unexplained.

*Inheritance of plant height and habit in the cross *Phaseolus vulgaris* × *multiflorus* and reciprocal*

MENDEL (74, 1865), without giving actual data, stated, that the plant height and twining habit of *Ph. multiflorus* dominate over the characters of *Ph. nanus*, the bush bean, and that the segregation in the first generation of the hybrid is conform to expectancy and considered as a simple 3 : 1 segregation.

TSCHERMAK (120, 1901; 122, 1904; 123, 1912) observed that in several crosses between *multiflorus* and bush beans the  $F_1$ -plants were more or less intermediate. Though the author did not distinguish between determinate and indeterminate growth, we may take it for granted that his  $F_1$  hybrids were of indeterminate growth, twining habit and only less tall than *multiflorus*. His  $F_2$  generations of both reciprocal crosses are following:

*Ph. multiflorus* × *vulgaris*. 26 tall; 118 short, bush type.

*Ph. vulgaris* × *multiflorus*. 18 tall, 2 intermediate, 35 short, bush type.

This is markedly different from what might be concluded from MENDEL's statement; and, indeed, it is quite unexpected as indeterminate growth dominated in  $F_1$ . That his  $F_2$  plants have not been protected against cross-fertilizing insects may have influenced the results, yet, as the bush bean type of growth is recessive, we should only expect a diminished number of bush types through spontaneous hybridisation. Among further generations we find:

from short types: 407 short: 57 tall; 81 short: 14 tall; 3 short: 1 tall.  
and in the reciprocal cross: 34 short : 1 tall; 58 short: 4 tall.  
from tall types: 22 short : 20 tall; 4 short : 14 tall; 23 short : 21 tall.  
and in the reciprocal cross (offspring of 5 indiv. taken together) 45 short : 23 interm. : 10 tall; and 100 short : 67 interm. : 44 tall.

These data cannot be reasonably brought back to any simple factorial scheme. Most probably spontaneous cross-fertilization has done much wrong (as is admitted by TSCHERMAK). On the other hand EMERSON's remark may be valuable: "While it is possible that the very irregular results secured by him are due to the fact that he dealt with a cross of very distinct species . . . it seems quite probable that they are due to failure to distinguish sharply between habit of growth and other factors of height". Yet another possibility might be advanced that I have nowhere found considered: a combination of linkage and non-viability, as in such hybrids of diminished fertility is by no means improbable.

TJEBBES (108, 1921), in a preliminary report, states dominance of the tall twining habit of *multiflorus*. The  $F_1$  generation is, however, not uniform but consists of two forms: giants and dwarfs. The characters of these dwarf and giant forms are apparently dependent on the *vulgaris* race that entered the cross.

female parent <i>vulgaris</i> race	dwarf $F_1$ offspring	giant $F_1$ offspring
van Celst's giant	very small, hardly viable	about like <i>multiflorus</i>
Chevrier, bush bean pure line Johannsen bush bean	c <sup>a</sup> 1 M c <sup>a</sup> 0.75 M.	several meters 8—10 meters

UPHOF (132, 1922) gives an account of the same material. As, however, TJEBBES (109, 1923) states that this has been published without his permission, that the facts are in several respects not correctly rendered, I confine myself to merely mentioning the paper.

It was however not the first time that dwarfs of this kind were observed. TSCHERMAK (120, 1901) crossed Wachsdattel (*vulgaris*, bush bean type, height 40—50 cm) with *Ph. multiflorus* (height about 3 m), and obtained 4  $F_1$  plants, measuring respectively 20 cm, 50 cm, 89 cm and 145 cm. In later generations (122, 1904) he observed a few dwarfs and giants.

TEN DOORNKAAT-KOOLMAN (18, 1927) also observed this twin na-

ture of the  $F_1$  generation. He obtained from his crosses the following numbers:

Saxonia (bush bean)  $\times$  multiflorus (red-flowered) 23 vigorous: 9 dwarf  
 Flageolet St. Andreas  $\times$  " white-flowered "Zar" 1 dwarf  
 Saxonia  $\times$  " " 16 vigorous : 6 dwarf.

The author considers the differences between giant and dwarf plants to be of a genotypical nature, not as mere modifications of a common genotype. He did not observe marked indications of sterility in these  $F_1$  plants, unless caused by the deficient condition of some dwarfs. That so few seeds were harvested (only 292 seeds from 55  $F_1$  plants) is mainly ascribed to lateness in ripening on account of the too luxuriant growth (heterosis). The  $F_2$  generations consisted together of 205 plants of which 5 could not be determined as pole or bush bean types. Of the remaining 200 plants 46 are described as pole beans, 154 as bush beans.

Of  $F_3$  data the following may be reproduced:

$F_2$  plants twining, pole bean type.

$F_3$  12 pole bean type : 6 bush bean type

15 id. : 8 id.

17 id. — (apparently constant).

$F_2$  plants non-twining, bush bean type.

$F_3$  3 pole bean type : 12 bush bean type

1 id. : 7 id.

3 id. : 4 id.

An analysis according to the principles of EMERSON is not given.

This marked parallelism between the results of TSCHERMAK and TEN DOORNKAAT-KOOLMAN makes a more detailed analysis desirable. Instead the latter author gives a classification of the different  $F_2$  and  $F_3$  types:

a. plants with apparently normal development.

1. bush bean type, like *vulgaris*.

2. bush bean type, like *multiflorus* or intermediate.

3. pole bean type, like *vulgaris*.

4. pole bean type, like *multiflorus*.

## b. giant plants

- 5. pole bean type, like *multiflorus*.
- 6. nearly non-twining, "creeping", like *multiflorus*.

## c. dwarf plants

- 7. with twining axis, normal leaves and flowers, like *multifl.*
- 8. non-twining, normal leaves and flowers, like *vulgaris*.
- 9. diseased dwarfs. Twining axis; abnormal leaves and flowers.

Type doubtful.

10. Like the former save that the axis is non-twining.

In the types 9 and 10 the author is inclined to see the effect of lethal genes that already partly were effective in some  $F_1$  generation plants.

From this classification, if I am not mistaken, it may be seen that apparently a good deal of the *vulgaris* characters on the one hand, of the *multiflorus* characters on the other hand seem to be associated to such an extent even, that nearly every rather normal plant can be considered to be either a *vulgaris* or a *multiflorus* type. Without closer analysis it is impossible to say whether this is correct, or whether only some few characteristics (for instance type of flower or inflorescence) made the author consider a plant as belonging to a certain type. Further some characters, like the twining habit are more or less independently inherited. Then, it is most remarkable that the giant plants are all *multiflorus*-like and that among the normal dwarfs those with a twining axis are like *multiflorus*, those with a non twining axis are like *vulgaris*.

One other point might be worth while further consideration. We shall see on p. 384, where the seed-coat colour factors are considered, that the common black mottled seed type of the scarlet Runner bean is possibly nearly always heterozygous for one of the colour factors (a—Au—Ad). As crosses of *Ph. vulgaris* and *Ph. multiflorus* in most cases also reveal the nature of the latter with respect to height factors, it might be interesting to arrange a series of experiments in which different *multiflorus* types (Au Ad, Au Au, Ad Ad) are involved, and to study the relations between self-fertility and the nature of the  $F_1$  generation with respect to plant height.

This twin nature seems to be rather firmly established. The fact that TEN DOORNAAT-KOOLMAN obtained 39 vigorous plant against 16 dwarfs instead of equal numbers is easily explained by the lesser viability of the latter.

## IV. FLOWER COLOUR

*Phaseolus vulgaris*

The observations concerning the inheritance of flower colour are many, yet there are only few statements that may be considered as final. This is a consequence of the extreme difficulty to distinguish between the perhaps numerous gradations in colour. As an example I might point to the colour types mentioned by MIYAKE a.o. (75, 1930) who depict 6 flowers with different dilutions of red. Besides the colour development is much influenced by the action of the sunlight, another important difficulty, extremely so where plants are isolated from insects by means of cloth covers.

Also the different denomination of the colours forms a serious hindrance. Thus SHAW and MIYAKE speak of red and pink, all other investigators of violet, lilac etc. As a matter of fact reddish as well as bluish colours exist.

TSCHERMAK (121, 1902) reports some preliminary data. In the crosses white-flowered Wachsschwert  $\times$  violet-flowered Non Plus ultra and  $\times$  violet-flowered Wachsdattel, the  $F_1$  plants had a more intense violet flower colour, that segregated in  $F_2$  as follows:

first cross: 26 dark violet, 28 violet, 25 pale violet, 19 white

second cross: 23 dark violet, 19 pale violet, 13 white.

EMERSON (20, 1904) reports also very summarily. "White color is correlated with white seed color and usually the darker the seed color the deeper the flowers are colored. Where seeds are white with but a small amount of color about the eye, the flowers are also sometimes white". "In hybrids between plants with deeply colored flowers and white-flowered plants, the dark color is usually dominant". He often observed a stronger coloration in  $F_1$  hybrids between white-flowered and slightly tinted-flowered plants, or between two such tinted ones. He considers only the segregation into coloured en white. (26 : 8; 13 : 7; 16 : 5; 6 : 1, 4 : 5, 10 : 4). Thus far the results might seem rather simple, an illusion that is immediately destroyed when we consider the results obtained by SHAW (94, 1913). This author distinguishes between the following types:

1. White. In most cases this is pure white. Red Valentine, however, may sometimes display a slightly pinkish and more or less waxy tinge.

2. Light pink; distinctly tinged with pink, especially on the keel, never waxy.
3. Pink, a deep shade of pink. Outside of banner petal uncoloured.
4. Purplish crimson. Occurs only in races like Blue Pod Butter, where the entire plant is deeply tinged with purple. The outside of the banner petal is purplish crimson.
5. Waxy pink, only appeared in crosses with Blue Pod Butter. The colour resembles that of light pink blossoms, the outside of the banner is darker pink. The whole plant is waxy brownish yellow.

The author simply gives a statement of the results obtained in different crosses without attempting a factorial analysis. MATSUURA tried to represent these results, equally without a factorial analysis. This must lead to misunderstandings. The results are so complicated that an analysis is impossible; only some general conclusions are allowed and even these need corroboration rather badly.

A summary of SHAW's data may be found in the following table, in which only types are indicated without actual figures.

TABLE 3.

Type of cross	F <sub>1</sub>	F <sub>2</sub>					Observations in F <sub>3</sub> and F <sub>4</sub>
		White	Light pink	Pink	Crim- son	Waxy pink	
Light Pink × white	Light pink	×	×				White in some cases breeds true, in others may segregate pink.
Light Pink × white	Light pink	×	×	×			White breeds true; light pink and pink may segregate white, light pink and pink.
Pink × White	Pink	×	×	×			White breeds true; pink may segregate pink and white.
Pink × white	Pink	×	×	×			White breeds true or segregates pink or light pink; light pink and pink may segregate white, light pink and pink.

Type of cross	F <sub>1</sub>	F <sub>2</sub>					Observations in F <sub>3</sub> and F <sub>4</sub>
		White	Light pink	Pink	Crimson	Waxy pink	
Crimson × white	Crimson	×	×	×	×	×	White may breed true or segregate light pink, pink, crimson, waxy pink in small numbers. The other colours may apparently segregate in small numbers all other colours, but mainly light pink → pink and white pink → white. Crimson → white, pink and waxy pink waxy pink → white and light pink.
Pink × light pink	Pink	×	×	×			Light pink and pink may segregate both types or breed true.
Crimson × light pink	Crimson		×	×	×	×	Light pink may breed true or segregate waxy pink. Pink may breed true or segregate light pink.
Crimson × Pink	Crimson	×	×	×	×		Crimson may breed true or segregate light pink, pink, crimson, waxy pink.
White × white	White Pink Light pink	×	×	×			Pink as well as crimson may breed true or segregate white, light pink, pink, crimson. White breeds true.
Light pink × light pink	Light pink id.		×			×	white, light pink and pink may breed true or segregate white, light pink, pink. breeds true.

Even without figures these data prove that either the factorial background of the flower colours or their separation, or both are extremely intricate. A segregation, apparently as simple as that of the cross Light pink  $\times$  white,  $F_2$  white and Light pink, shows (data of 13 crosses taken together) segregation into 527 light pink and 229 white (40 : 8; 71 : 22; 19 : 9; 67 : 17; 47 : 15; 88 : 61; 34 : 26; 34 : 5; 25 : 16; 53 : 24; 22 : 9; 27 : 17). It cannot be explained as a monohybrid segregation, not even as partly monohybrid, partly dihybrid one, as some whites may segregate light pink. In most other crosses the matter is still more complicate. Only some provisional general conclusions are possible. As whites, when intercrossed, may produce coloured offspring at least two factors must cooperate for the production of flower pigment. White flower colour is associated with white or eyed seed-coat. From table 3 the dominance relations of most colours may to some extent be seen. Perhaps inhibiting factors are involved. Crimson flower colour is associated with Blue Pod Butter characters (buff seed coat, general purple pigmentation of entire plant). Most probably there is a one factor (or group of linked factors) difference between crimson and waxy pink. Further, according to SHAW and NORTON (95, 1918) most pigmented beans, with the exception of Red Valentine, have coloured flowers, though some commercial varieties have pigmented seeds and white flowers. Black and pink go always together unless in eyed beans.

JOHANNSEN (48a, 1913) mentions a cross between a white-flowered yellow-brown seeded race and a violet-flowered black seeded one.  $F_1$  black seeds, violet flowers.  $F_2$  gave a simple dihybrid segregation. White-flowered, yellow-brown seeds 39, wh. flowered coffee-brown seeds 121, violet-flowered, bluish purple seeds 105, violet-flowered, black seeds 293.

TJEBBES and KOOIMAN (115, 1921) give some results on a spontaneous violet-flowered hybrid of a light lilac-flowered race. In  $F_2$  segregation occurred into white, light lilac and violet (dark and light) in a ratio 1 : 1 : 2. The flower colours were in a way associated with the seed coat colours and the striping colours of the pods.

Pod colour	Flower colour	Seed-coat colour
blue	dark or light violet	black or bluish grey
blue	dark violet	blue-purple

blue	dark or light violet	violet
red	lilac	brownish black, reddish grey or red
pale blue	white	white
pale red	white	white.

This may be explained by the assumption that a factor R causes the red colour of pod striping in the absence or presence of the groundfactor for seed-coat colour A. When this A is present the flower colour is lilac, the seed-coat colour red (a black factor changes this colour) by the action of factor R. These colours are changed into bluish tints by the action of Bl. The difference between light and dark violet flower colour is apparently that light violet is Bl bl.

The same authors (117, 1922) state that yellow-brown beans may have white, lilac or violet flower colours.

They further report on some observations with respect to observed relations of flower colour and seed coat colour in  $F_4$  families of a cross between a violet-flowered yellow-brown and a white-flowered bean in which the factors A, B, C, D, E and F (see pages 330 sq.) are involved. Of these factors A is the ground factor (ferment factor) without which no colour is possible, B, C and D are chromogenous in collaboration with A; E and F are intensifiers. Provisionally it is stated that for the realisation of flower colour one of the combinations AB, AC and AD is necessary and that besides the intensifier F is afforded. Yet there is still another factor causing flower pigmentation that does not affect the seed coat colour. This factor is responsible for white and yellow-brown seeded races with coloured flowers. (see also FRUWIRTH, 32, 1924).

MIYAKE a. o. (75, 1930) distinguish as main types red, pink, "flecked" (colour distributed as small stripes along the veins of the wings) and white. They state that pink and flecked are simple recessives to red. Pink  $\times$  flecked and white  $\times$  red give 9 : 3 : 4 segregations in  $F_2$ . A certain relation between stem colour and flower colour is stated. Pink stem colour is associated with pink flower colour, red stem colour with red flower colour; green stem colour may go together with any of the described types of flower colour. A rather simple solution might be suggested, but for a defective representation of the data and a serious inconsistency between the tables V and IX.

*Flower colour in Ph. multiflorus*

Within the species *Ph. multiflorus* three main different flower colours may be distinguished, white, scarlet, and white wings, scarlet banner petal.

The relation between scarlet and white is quite simple. In crosses between both types scarlet is fully dominant. In  $F_2$  a clear cut 3 : 1 segregation occurs. In a cross between a scarlet-flowered race and a bicoloured one (scarlet banner, wings pale rose coloured) scarlet is dominant though the  $F_1$  colour is slightly lighter (TSCHERMAK 122, 1904).

*Flower colour in Ph. vulgaris × multiflorus*

In crosses between the species *Ph. vulgaris* and scarlet-flowered *multiflorus* the flowers of the  $F_1$  hybrids are described by all authors as less intensively red, more salmon-coloured (for accurate description see TEN DOORNKAAT-KOOLMAN, 18, 1927, p. 158). With respect to the flower colour in crosses with white-flowered *multiflorus* no reliable data are furnished. With respect to  $F_2$  data we have only summary descriptions at hand. Thus MENDEL, who crossed a scarlet *multiflorus* with a white *vulgaris* race observed one white-flowered plant among 31  $F_2$  offspring and described the other colours as of various grades of purple-red to pale violet. TEN DOORNKAAT-KOOLMAN describes the  $F_2$  colours as: light violet, scarlet, white with pale or stronger venation of banner and wings, light yellow, salmon-coloured, rose-coloured, banner and wings with white margin, dark violet, and all kinds of transitions between these colours.

TSCHERMAK (123, 1912) gives a summary of earlier observations. One of his crosses which was more or less accurately guarded against cross-fertilising insects may be rendered here:

*Ph. vulgaris* (pale lilac) × *multiflorus* (yellowish red).

$F_1$  salmon-coloured

$F_2$	14 pale lilac	5 pure red	19 yellowish red			
$F_3$	constant	segregating into pale li- lac and red	segregating into pale lilac, red	segregating into pale lilac and yellow- ish red.	segregating into pale lilac, red	segregating into pale lilac and yellow- ish red.

## V. POD CHARACTERS

*Pod form*

The pod-form is apparently determined by a good number of factors, most of which are of a quantitative nature (long vs. short; broad vs. narrow; length of apex; degree of constriction; degree of curvation). An insight in these matters is of course not possible before a special analysis (phaenogenetical and genetical) has to a satisfactory degree revealed these formative factors and their interrelations. That such interrelations exist may be apparent from a fact observed by TSCHERMAK. This author crossed Zucker Reisperl, with constricted pods as a seed parent, with a large-seeded race and observed that the pod containing the hybrid seeds was inflated instead of constricted. This proves that a relation between seed dimensions and constriction exists. On the other hand a relation between pod constriction and texture of the pod wall is well-known.

As yet only few such characters have been considered in genetical investigation. MENDEL (74, 1865) in his bean cross observed dominance of inflated pods, 3 : 1 segregation in  $F_2$  and independence from plant height and pod color. TSCHERMAK (121, 1902, 124, 1916) gives the following statement: Round dominates over flat; blunt apex prevails over sharp apex; broad prevails over narrow; long prevails over short. In the first case 3 : 1 segregation was observed in  $F_2$ ; for all other cases he reports "impure segregation", which suggests that more factors are involved. The same author (129, 1922) observed dominance of inflated over constricted pods (actual numbers 78 inflated : 16 constricted). In these figures he sees indications for a two factor difference. This seems rather too simple in consideration of his remark that apparently a certain correlation exists between seed weight, seed form and the constricted-inflated character.

Equally the results of WÓYCICKI (137, 1928) cannot be considered as very satisfactory. This author consider the pod characters length, breadth and width. Furthermore the degree of flatness ( $F$ ) =  $\frac{B}{D}$ , in which  $B$  = breadth,  $D$  = width; and  $W$  (= "Welligkeit", degree

of constrictedness) =  $\frac{D}{d}$ , in which D = width of pod at the seed locations, d, width between seed locations.

In one cross (Królowa  $\times$  Japónska) the  $F_2$  segregation is considered to point to the following factorial differences between both races:

With respect to length 3 cumulative factors.

“	“	“	breadth 2	“	“
“	“	“	width 2	“	“
“	“	“	constrictedness 1	“	“
“	“	“	flatness, all factors for breadth and width influence this compound character.		

In this cross the graphical representation shows clearly marked tops. This is not the case in a second cross between Riccardianus and Japónska, with respect to length, breadth and width. Here transgressive segregation is observed.

The author further observed correlations between length and breadth, length and number of ovula; from the latter Wójcicki concludes that no correlation exists between length and distance of ovula, in connection with his earlier observation (137a, 1924) of the occurrence of deformed seeds in hybrids, on account of a dis-harmony of distance between the ovula and seed dimensions.

TEN DOORNKAAT-KOOLMAN (18, 1927) gives merely some illustrations of pod forms resulting from certain crosses, without attempting an analysis.

In the cross *Ph. vulgaris*  $\times$  *multiflorus* and reciprocal the pod characters of *Ph. multiflorus* dominate in  $F_1$ . In  $F_2$  segregation occurs and many combinations of parental characters are observed (TSCHER-MAK 122, 1904). According to TEN DOORNKAAT-KOOLMAN the coarse surface of the *multiflorus* pods is frequent in  $F_2$ , whereas the *vulgaris* type is only seldom realised.

#### *Parchmented vs tender pod walls*

In most wild leguminous plants the pod walls are parchmented. This parchment consists of fibers which run obliquely across the pod wall from suture to suture. In young pods it is at first absent, but develops gradually as the pod matures. In beans this must have been the original condition. There is however a wide range of variation in

the development of this character. Some races are outspoken parchmented, other ones are tender, developing no parchment at all or only late. Between these extremes different stages of parchment development occur.

EMERSON (20, 1904) considered the estimation of this character to be extremely difficult. In the  $F_1$  of a cross between a tender-podded and a parchmented race the development of parchment fibers was nearly suppressed in some cases, in other cases it was intermediate.

TJEBBES and KOOIMAN (117, 1922) observed dominance of the parchmented type and in  $F_2$  174 parchmented : 37 tender. Of 174 parchmented plants, 37 proved to be homozygous, 130 segregated (7 gave no offspring). The total numbers of parchmented and tender offspring of these 130  $F_3$  generations were 1572 : 512. This made the authors suggest a monofactorial segregation.

#### *Stringiness of pod*

The first investigations on this character are by EMERSON (19, 1902; 20, 1904). In most of his crosses he found complete or nearly complete dominance of stringlessness. In these cases  $F_2$  showed segregation into stringless and stringy. In  $F_3$  all stringy and part of the stringless types bred true, the other stringless ones segregating as did the  $F_2$ . In both  $F_2$  and  $F_3$  the number of stringless plants was less than might be expected according to a 3 : 1 segregation.

In some crosses, where Navy, Curry and Red Valentine were the stringy parent, the stringiness of the  $F_1$  was more or less intermediate. In  $F_2$  segregation into stringy, intermediate and stringless occurred, the classification being rather difficult (data of three crosses taken together: 114 stringless; 80 intermediate; 78 stringy). In  $F_3$  some stringy as well as some stringless plants bred true, some stringy and stringless plants, and besides all intermediate ones segregated:

	Stringless	intermediate	stringy
7 intermediates . . . . .	47	16	38
5 stringless . . . . .	42	9	16
4 stringy . . . . .	20	1	54

Though difficulties of classification have doubtless influenced these numbers to some extent, the character is evidently rather complex, as there is strong indication of difference in dominance of stringlessness.

WELLENSIEK (135, 1922) made crosses between (1) Hinrich's Riesen (stringless) (2) "Volgers" (stringless) (3) Chocolate brown (stringless) and stringy Wagenaar. He records stringless as dominant and a clear-cut 3 : 1 segregation in  $F_2$ .

JOOSTEN's analysis (50, 1927) of the same material shows us that the problem is much more complicated. Originally he distinguished 4 classes of stringiness: stringless, string doubtful, stringy, very stringy. As the purpose of his work was the breeding of a stringless race from crosses of stringless and stringy varieties, offspring of the first two classes only of  $F_2$ — $F_4$  plants was bred. No single family, however, proved to be entirely stringless, the majority of the plants in every case even being stringy. It is furthermore shown that not one of the so-called stringless races, as offered by the trade, deserves this epithet. In later years JOOSTEN refined his classification; he distinguished 10 classes (string numbers 1—10). In classes 1—6 the string is not continuous, as it is in classes 7—10. Microscopical investigation shows that there is a marked degree of parallelism between these string numbers and the anatomical structure of the suture fibers. The great variations in stringiness with age and perhaps also with environmental influences make an analysis difficult. There are here, as in part of Emerson's crosses, indications of dominance of stringiness in some cases.

#### *Pod colour*

The general colour of the unripe pod may be either yellow or green, displaying in the latter case different shades from light to bluish green. Besides the pods may be striped either entirely or at the apex only, with a reddish or bluish violet. Even the whole pod may be entirely tinged with purple.

The yellow-podded beans, eventually tinged with violet, are distinguished as wax beans. This yellow colour is caused by a comparatively early loss of chlorophyll, which loss in other than wax varieties only occurs after the pod is fullgrown. Wax varieties however vary considerably in this character, some races losing their chlorophyll

very early, whereas other ones never quite lose it before ripening.

Crosses of Wax varieties with green-podded ones have been carried out by several experimenters. MENDEL (74, 1865) simply states dominance of green, 3 : 1 segregation in  $F_2$  and independence from plant height and pod form. All later investigators invariably came to the same conclusion: TSCHERMAK (121, 1902); EMERSON (20, 1904); LOCK (65, 1906), TEN DOORNAAT KOOLMAN (18, 1927).

The same simple relation exists between the green-podded *Ph. multiflorus* and wax bean varieties of *Ph. vulgaris*. (TSCHERMAK 121, 1902 p. 858; 122, 1904, p. 613).

Blue green is dominant to green (EMERSON, 20, 1904). In some races the pod as well as the whole plant is entirely tinged with purple. SHAW and NORTON (95, 1918) state that in crosses with Blue Pod Butter the combination of buff coloured seeds, purple foliage and pods, and crimson flowers reappears in about one fourth of the offspring.

EMERSON (20, 1904) considers the purple colour, that usually appears as spots and splashes (stripes) on a ground colour of green or yellow. Crosses between striped and non-striped races were not made. "In several cases, however, hybrids have had their pods strongly colored with purple, and this has occurred in hybrids between two yellow-podded races, between two green-podded races, and between a yellow-podded race and a green-podded one neither of which is marked in this way though all of them may occasionally have a few specks of purple near the tip end of the pods". EMERSON considers it to be a heterozygous condition.

I don't know whether in some cases this may be true. Equally I don't know whether such striping may occur independently of other characters, or whether it is always correlated with certain seed-coat characters. This should be further investigated.

In the cross between Dwarf Cranberry Bean ♀ and a yellow bean such a correlation doubtless exists. In the dwarf Cranberry bean, at least in the race used by TJEBBES and KOOIMAN (113, 1919), also according to the description by DENAFFE, the pods are strongly striped with purple. The  $F_1$  hybrid between both races had the pods striped like the seed parent. In  $F_2$  segregation occurred in striped- and green-podded plants in a 3 : 1 ratio (69 : 22) and all green-podded plants had self-coloured seeds, whereas the plants with striped pods

had also striped seeds. This points either to a strong linkage or identity of the factors causing striping of pods and seed-coat in this case.

This striping of the pods is often seen in races belonging to the horticultural type and is not always accompanied by a coloured seed-coat. TJEBBES selected from Hinrichs Riesen a white seeded strain with bluish striped pods. In a spontaneous cross between the Cranberry Pole bean with red striped pods and this white-seeded race, the  $F_1$  had the pods striped with dark blue. In  $F_2$  segregation occurred into dark blue, light blue, red and pale red. The explanation given by TJEBBES and KOIMAN (115, 1921; 116, 1922) is no longer considered by them to be correct. Both types are now considered to have factor S (for striping) in common. The difference between dark blue and red is Bl as indicated, that between dark blue and red on the one side and light blue and pale red on the other side is merely caused by an intensifier. There is the following relation between pod-colour, flower-colour and seed-coat colour:

Genotype	Colour of pod striping	Colour of seed-coat striping	Flower colour
aa RRSS bl bl	pale red	white	white
aa RRSS Bl	pale blue	id.	id.
A RRSS bl bl	red	brownish black,	lilac
id.	id.	greyish red	id.
id.	id.	red	id.
A RRSS Bl	blue	black to violet	light to dark violet.

The differences in the red series (brownish black, greyish red and red) as well as in the blue series (black, greyish blue, purple, violet) must be ascribed to at least one modifier (factor Z).

## VI. PIGMENTATION OF THE SEED-COAT

*Seed coat colour in Phaseolus vulgaris*

The seed-coat of beans may be either colourless (or at best slightly tinged with ivory-white), or it may be entirely or partly coloured by pigments situated in the testa.

KAJANUS (51, 1914) states that black, blue, dark green, greenish-brown are caused by pigment granules filling the lumina of the palisade cells. They are insoluble in cold water. Purplish (violet) pigment, equally localised in these cells is soluble in water. Lemon colour is found as a homogenous pigment filling the lumina of the palisade-cells, non-soluble in cold water. Orange-brown and brownish-yellow seem to be situated in the palissade-cell-walls. They are soluble in cold water. The reddish yellow ground-colour is caused by a yellowish granulous pigment of the second, parenchymatous cell-layer. The light green colour (e.g. of Chevrier's Flageolet) is caused by green granules in the same layer (chlorophyl).

TJEBBES and KOOIMAN (113, 1919) also observed that pigments may be situated in the prismatic as well as in the parenchymatous layers. In the Cranberry bean (Kievitsboon) the brown pigmentation of the parenchyma fails, the stripes show a purplish-red pigment in the prismatic cells of the outer layer side by side with single cells containing brown pigment. In the yellow-brown bean only brown pigment occurs. In the hybrid sharply distinguishable fields of brown, purplish and colourless cells were observed. The colours are more or less soluble in boiling water, giving a dark red-brown decoct. The same decoct however is obtained from the colourless parts of the seed coat of the Cranberry bean, which seems to point to a local suppression of the development of pigment in that race.

In black-mottled seeds the contents of the prismatic cells was found to be partly colourless, partly dark blue, with isolated dark brown cells. In blue-mottled seeds the situation is nearly like in black-mottled ones, the blue colour is more dilute, rather violetish and brown cells fail.

In brown-mottled seeds the seed-coat is partly colourless, partly dark brown, partly light brown with isolated brownish violet cells.

In violet-brown mottled seeds the coloured cells are violet-brown.

With  $H_2O_2$  the blue colours change into brown.

SHAW and NORTON (95, 1918) distinguish two colour-classes:

1. The red series, consisting of red and purplish red pigments, soluble in water. Red changes into purplish red when treated with alkali; purplish red into red in acid solutions.

This points to their being anthocyanine pigments.

2. The yellow-black series, consisting of yellow, coffee-brown and black. The pigments are considered to be only slightly or perhaps not at all soluble in (cold) water, but soluble in alcohol and alkalies.

SKALINSKA extracted the pigments with alcohol and found the following chemical nature:

in extracts from black and violet: anthocyanines,

in extracts from yellow: a pseudobase, originating from an isomerised anthocyanine,

in extracts of yellowish and brown: only traces of pseudobases, mainly flavonols, which in the presence of chlorhydric acid at an elevated temperature change into anthocyanine.

In old bean seeds of yellowish and yellow varieties the pigment changes into brown. This is a process of oxidation. Equally acid alcoholic solutions of anthocyanine change with time into brown.

The author consequently considers the interrelation of the pigments mentioned as follows:

„Donc, toute la série des pigments mentionnés présente le produit de diverses transformations d'un seul composé; or, les facteurs génétiques à la présence desquels sont du les changements de pigmentation ont des rôles chimiques définis: les uns conditionnent une réduction de flavonol, d'autres une acidification du suc cellulaire, d'autres contribuent à l'isomérisation de l'anthocyane par la neutralisation du suc cellulaire, etc.”

These observations may be considered to give satisfactory indications that nearly all seed-coat colours are chemically related. Yet many problems remain to be solved, though these problems are perhaps more of a general physiological and phaenogenetical than of a strictly genetical order, like e.g. the occurrence of several pigments, side by side and often in two partly overlapping patterns. It might be also interesting to know the chemical nature of the contents of the prismatic cells of white and ecru seeded races.

In many respects our knowledge is too fragmentary to see the close parallelism which necessarily must exist between the genetical and the chemical nature of the pigments. Yet there are unmistakable indications as to such a parallelism in the observations by SHAW and NORTON. These experimenters used rather extensively a bean variety Blue Pod Butter, which is characterized by buff-coloured seeds. This variety, when crossed with either a race of the red series or of the yellow-black series, behaves as a simple recessive, the  $F_2$  consisting in all cases of about one fourth of plants with cream coloured seeds. When a race of the red series is crossed with one of the yellow-black series, both colours show in  $F_1$ . In  $F_2$  representatives of both series and types like  $F_1$  are segregated and besides in small numbers buff-coloured ones, but never white. This lead to the assumption that the red and yellow-black series have the factor or factors for buff-colour in common, further that the red series on the one hand, the yellow-black series on the other hand are determined by different factors that are genetically linked. These factors have been termed the *red modifier* and the *yellow-black modifier*. The colours which the seed-coat will actually display are determined by factors, termed by SHAW and NORTON determiners. We consequently get the following scheme:

Groundfactor absent	White	P	
Groundfactor present	Buff	P	
Action of modifiers M and M'	Yellow-black series	PM	PM' Red series
Action of determiners	Yellow	PMC	PM'D Light red
	Coffee-brown	PMG	PM'E Dark red
	Black	PMF	

Principally this statement may be accepted as a working hypothesis. Factor P has been used by most experimenters, yet this P, as will be shown lateron, is not to be considered as a single factor but as one of a series of factor combinations.

KOOIMAN (56, 1920) gives a different statement that only covers the yellow-black series. As two whites may sometimes, when intercrossed, give coloured offspring (observations by SHAW and NORTON) and as sometimes two intercrossed coloured-seeded races may in  $F_2$  segregate some whites, a two factor hypothesis for the realisation of

simplest colours is advanced. Factor A is considered to be a ferment factor, inactive but in the presence of one of three recognized chromogenous factors B, C and D. These simplest colours may be modified by determiners (intensifiers) E and F. Another paper by TJEBBES and KOOIMAN furnishes the facts to insert a red series into this scheme. A cross between a yellow-brown seeded race and a red striped one led to the assumption that red and striped are linked and that red-striped and one of the factors of the yellow-black series show absolute repulsion. Here cream is not segregated. We consequently arrive at the following scheme:

Groundfactor for colour

(Ferment factor) A. White

Chromogenous factors,

active with A	AB-ABC-AC	AD	AR
	Yellow-black series	Smoky white with coloured hilum ring	Red series
Colour determiners	E Brown-factor		Bl, Blue-factor.
	F Violet-factor		
	EF Blackening combination.		

The main difference between both schemes is apparently:

That a necessity to assume special modifiers has not been felt by KOOIMAN. As a matter of fact no single observation has come to the attention of the reviewer that opposes against the identity of any of these assumed modifiers with a determiner. Thus KOOIMAN's chromogenous factors, at least four in number, take up the combined role of the modifiers and part of the determiners assumed by SHAW and NORTON (M'D and MC). A consequence of the hypothesis of the latter is that in no cross between a representant of the red series and one of the yellow-black series whites may be segregated. According to KOOIMAN's hypothesis many such crosses are possible. As a matter of fact such a cross has been observed by SIRKS (100, 1922), who reports the segregation of whites in a ratio of 15 coloured: 1 white from a cross between a race with lemon-coloured seeds and a red-mottled race (Kievitsboon, in this case a really mottled, not a striped race).

Besides the green colour (1), which is not considered above, the foregoing reveals the following colour groups that may be separately considered:

- (2) White.
- (3) The ground-colour, or parenchymatic colour (buff or ecru).
- (4) The yellow-black series.
- (5) The red series.

(1) *The green colour*

In some races, like Chevrier's Flageolet the testa as well as the seed-lobes are green, on account of the presence of chlorophyl. This colour rapidly fades away when exposed to day-light. (See also FRUWIRTH, 31a, 1909). As this occurs easier in the testa than in the seed-lobes, segregation observed on the latter will give more trustworthy data.

TSCHERMAK (122, 1904, p. 564—67, 582) observed in crosses of Chevrier ♀ × races with yellow seed-lobes (Non Plus Ultra, Schirmers Cassler, Bunte Ilsenburger and Weisse Ilsenburger), that the seed-lobes of the SG<sub>1</sub>-seeds were white (Xenia cp. also TSCHERMAK 131, 1931). With respect to seed-lobe colour 3 : 1 segregation was found. Lateron (128, 1920) the same author reports on numerically larger data. Again he finds 3 : 1 segregation (actual figures 810 : 239

$$= 3.088 : 0.912; \sigma = \pm 0.053 \quad D = \frac{0.088}{0.053} \quad \text{KOOIMAN (128, 1920)}$$

observed the following segregation from a spontaneous hybrid of Chevrier: coloured 25; white 7; green 2; and with respect to seed-lobe colour 3 : 1 segregation.

TSCHERMAK furthermore observed that the seeds with green cotyledons lose their chlorophyll from the seed-lobes entirely at germination so that the young plantlets show white seed-lobes. Just the reverse is observed in seeds with yellow (white) cotyledons, that rapidly develop chlorophyl and consequently germinate with green seed-lobes.

2. *White*

White as a seed-coat colour is very common and the number of observations of its hereditary character are numerous. In all cases it behaves as a recessive to all coloured races, with the exception of green. In nearly all of the segregations observed white seems to behave as a simple recessive, differing in only one single fundamental factor from all coloured types. That this cannot be true for all cases was stated by SHAW and NORTON (95, 1918, p. 65): „The appearance of pigment in the seed coat is usually the expression of a complex-factor or the concurrence of several factors. In the absence of any one of the

elements of this factor complex the beans are unpigmented". Their cross of two whites: Davis Wax  $\times$  Michigan White Wax produced coloured offspring.

This statement, no doubt, is correct. The concurrence of at least two factors is necessary for the production of seed-coat colour. In a case, analysed by KOOIMAN (56, 1920) a far more complex situation was encountered. To explain the very complicate segregation it was necessary to put forward the hypothesis that the following factors concurred:

A, a groundfactor for colour. In the absence of A no colour is realised

B, C and D three chromogenous factors, any of which causes, in concurrence with A, pigmentation. The effect of any of these factors is distinguishable, though sometimes with difficulty. This hypothesis is of much interest for the coloured: white segregation, as may be seen from Table 6.

TABLE 6

Group	Genotypes of coloured: white segregating types	Scheme of segregation in $F_2$ families	Relative frequency
I	All Aa homozygous for one or more of the factors B, C and D AA Bb cc dd AA bb Cc dd AA bb cc Dd	3 : 1	80/256
II	AA Bb Cc dd AA Bb cc Dd AA bb Cc Dd	15 : 1	12/256
III	AA Bb Cc Dd	63 : 1	8/256
IV	Aa Bb cc dd Aa bb Cc dd Aa bb cc Dd	9 : 7	12/256
V	Aa Bb Cc dd Aa Bb cc Dd Aa bb Cc Dd	45 : 19	24/256
VI	Aa Bb Cc Dd	189 : 67	16/256 Identical to $F_2$ -segregation.
	several non-segregating types		104/256

In this table the complicated  $F_2$  segregation into coloured and white is given as well as the  $F_3$ -generations from the entire  $F_2$ -generation. Here we see that a 189 : 67 segregation, which unless in a very large population cannot be distinguished from a 3 : 1 segregation, gives rise to several, partly clearly distinct ratios in the following generation. Of these 45 : 19 and 189 : 67 again approach the 3 : 1 scheme too closely to be distinguished from it in the small  $F_3$ -generations usually cultivated. These three schemes together have a frequency of 120/256 as against 30/256 of the doubtlessly aberrant schemes 15 : 1, 63 : 1 and 9 : 7. Though the small  $F_3$ -generations grown by KOOIMAN do not permit a verification of the hypothesis in every detail, the results of a statistical analysis together with a factorial analysis along other lines shows that the data can hardly be well explained in any other way.

It has already been pointed out that these complicated coloured:white segregations closely resemble the 3 : 1 scheme. Further it may be stressed that frequently a limited number of usually small  $F_3$ -generations are grown and that such  $F_3$ -generations are often counted together. That this is misleading is apparent from the foregoing. In the first place small  $F_3$  generations hardly ever will reveal a 63 : 1 segregation, in many cases not even 15 : 1. In the second place, as (in the example cited) 4/5 of the  $F_3$  generations segregate according to 3 : 1 or nearly 3 : 1, the probability that unmistakably deviating ratios are revealed is still further diminished. In the third place the addition of small segregating families is generally inclined to lead to errors if not carefully done, in the present case the more so as the expectation for the combined segregating  $F_3$ -generations closely approaches the 3 : 1 ratio (actually 3.02 coloured : 0.98 white).

All experimenters who have used white beans in their crosses have experienced that such white beans generally bear several latent factors influencing the seed coat colour as soon as the factors, which enable the development of pigment, are supplied. White beans, recessive for all chromogenous factors have perhaps never been used. A consequence of this circumstance is that in most crosses between coloured and white beans,  $F_2$  segregations will usually be rather complicated and resemble 3 : 1 segregations. As a matter of fact most segregations reported support this view, as may be seen in Table 7. Only some observations by SIRKS (1900, 1922) upon spontaneous hy-

brids reveal deviating ratios. As such 251 : 18; 37 : 3 and 28 : 1 have to be considered. Most probably they are of the 15 : 1 type.

TABLE 7.

Cross	$F_2$ segregation	Author
Wachsschwert × Non Plus Ultra .	330 : 99	TSCHERMAK 1902; 1904.
Non Plus Ultra × Weisse Ilsenburger	7 : 5	"
Chevrier × Non Plus Ultra . . . . .	20 : 12	"
Mettes Schlachtschwert × Wachsdat- tel . . . . .	42 : 13	TSCHERMAK 1904.
Chevrier × Schirmers Casseler . . .	36 : 9	"
Mettes Schlachtschwert × Hundert für Eine . . . . .	35 : 13	"
Chevrier × Bunte Ilsenburger . . .	10 : 2	"
Weisse Wachs × Runde violettge- äugte . . . . .	57 : 27	TSCHERMAK 1912.
Runde rotviolettgeäugte × Weisse Ilsenburger . . . . .	38 : 13	"
Navy × Challenge Black Wax . . .	20 : 10	EMERSON, 1904.
id. $F_3$ from $F_2$ self-coloured . . . . .	80 : 29	"
Scarlet Flageolet × Davis Wax . .	7 : 4	EMERSON, 1909.
Challenge Black Wax × Davis Wax.	27 : 7	"
Davis Wax × Blue Pod Butter . .	22 : 12	"
Davis Wax × Non Plus Ultra . . .	41 : 20	"
White Marrow × Non Plus Ultra . .	29 : 15	"
Non Plus Ultra × Navy . . . . .	19 : 4	"
Navy × Challenge Black Wax . . .	20 : 8	"
White Marrow × Paris . . . . .	39 : 13	"
Navy × Paris . . . . .	52 : 12	"
Ne plus ultra × White Flageolet . .	337 : 105	SHULL, 1908.
Long Yellow Six Weeks × White Flageolet . . . . .	411 : 160	"
Prolific Black Wax × White Flag- eolet . . . . .	112 : 44	"

TABLE 7 (con<sup>d</sup>.)

Cross	F <sub>2</sub> segregation	Author
Spontaneous hybrid 2 . . . . .	52 : 12	KAJANUS, 1914.
"      3 . . . . .	10 : 4	"
"      4 . . . . .	62 : 26	"
"      5 . . . . .	33 : 11	"
"      6 . . . . .	66 : 32	"
"      7 . . . . .	22 : 12	"
"      8 . . . . .	20 : 7	"
"      9 . . . . .	61 : 17	"
"      12 . . . . .	17 : 4	"
Spontaneous hybrid from Pole Cran- berry Bean . . . . .	33 : 11	TJEBBES & KOOR- MAN, 1921.
Citroen × Kievitsboon . . . . .	251 : 18	SIRKS, 1922.
Yellow × White bean . . . . .	279 : 87	"
Yellow × white? . . . . .	37 : 3	"
Yellow × white . . . . .	149 : 48	"
Lemon-coloured yellow × white? .	28 : 1	"
Improved Yellow Eye × White . .	269 : 80	SAX, 1923.
id. . . . .	138 : 41	"
Dot Eye × White . . . . .	222 : 67	"
White × Mottled . . . . .	73 : 26	MIYAKE a.o. 1930.
White × Cream . . . . .	57 : 18	"
White × Cream . . . . .	79 : 35	"

In this table the data recorded by SHAW and NORTON have not been considered. It is much to be regretted that these are not liable to analysis in this as well as many other respects, where reliable ratios are requested <sup>1)</sup>.

<sup>1)</sup> The paper of SHAW and NORTON (95, 1918) is with respect to actual figures absolutely unreliable as a careful comparison of the tables shows. The same cross is represented in several tables, with respect to different characters. Thus we may find the segregation into coloured and white for one and the same cross in tables considering the segregation into coloured and white, into mottled, self-coloured and white, into eyed, totally pigmented and white.

### 3. *The parenchymatic colours*

These colours form the background in nearly all mottled and striped beans and besides occur in many self-coloured ones. Different authors indicated it with different names, and, as comparison is impossible we can only suggest with a reasonable degree of probability that such denominations as cream, ecru, chamois and buff refer to identical or at least related colours. Seeds belonging to this colour-group are always characterized by a darker coloured strophiolum and small ring around the hilum. Otherwise, though differences in shade occur, the ecru group is scarcely influenced by colour determiners. SHAW and NORTON (95, 1918) consider the buff colour to constitute the basic pigment of both the red and the yellow-black series. Now that we know that at least two different cream types exist, this remains to be verified, the more so as their buff-coloured variety, Blue Pod Butter, is a peculiar race that displays an apparently absolutely associated combination of the characters: crimson flowers, purple tinge of entire plant and buff seed-coat colour. When crossed with other coloured-seeded varieties the  $F_1$  consists of coloured beans segregating into 3 non-buff : 1 buff and all these extracted buffs have the Blue Pod Butter combination of characters. Consequently Blue Pod Butter misses a factor that is essential for the production of colours belonging to either the red or yellow-black series, and this factor is absolutely linked to a factor or group of factors that cause the production of crimson flowers and purple foliage.

In crosses of Blue Pod Butter with various races belonging to the yellow-black series as well as with those belonging to the red series in  $F_2$   $1/4$  of buffs are segregated but never whites. In crosses between a race belonging to the yellow-black series with a red-seeded race we might expect that no whites appear and, in case of independence of the modifiers of the red and yellow-black series, segregation into nonbuff: buff according to 15 : 1. As a matter of fact the segregation of small numbers of buff seeds is recorded; actual data, however, are not given. It will be shown lateron (see p. 355 sq.) that an explanation of this segregation of buff-seeded plants meets with considerable difficulties.

These figures differ in so many cases and sometimes so fundamentally that an objective use is out of the matter. I may cite one example. Cross No. 33 Table I, p. 66 states as coloured: white = 77 : 35. In table V, p. 72 the same cross is recorded as coloured (mottled + self-coloured) : white = 91 : 22.

In crosses of Blue Pod Butter with white-seeded varieties, the  $F_1$  plants are coloured-seeded, segregating in  $F_2$  about  $1/4$  of white-seeded plants. The proportion of buff among coloured beans is not stated.

From crosses of yellow- and brown-seeded races with Blue Pod Butter, giving in  $F_1$  and  $F_2$  black and coffee-brown seed-coat colours, it may be concluded that Blue Pod Butter carries determiners in a cryptomerical state. Consequently the buff or cream colour does not constitute a genetical unity any more than white does. This is strikingly apparent from a cross of two different cream-coloured races, a greyish and a yellowish cream, by MIYAKE a.o. (75, 1930). In this cross the  $F_1$  plants had black-purple mottled seeds. In  $F_2$  the segregation was as follows:

TABLE 8.

Cross	Mottled black-purple	Self-coloured black-purple	Greyish cream	Yellowish cream
1	66	29	51	17
2	39	18	39	11
Total. . . . .	105	47	90	28

From this we may see that greyish cream is essentially a simple dominant to yellowish cream. Furthermore that the segregation with respect to non-cream vs. cream (152 : 118) accords exactly with a 9 : 7 ratio and that no whites appear. We may conclude that both cream types have a common factorial basis but that either of the two cream races used in the cross have carried a factor cryptomerically, the concurrence of which is necessary for the production of colours other than cream. Such creams, when crossed with other self-coloured and mottled races should give a non-cream  $F_1$ . In  $F_2$  creams should appear in about  $1/4$  of the offspring. This apparently is the case with the only one of these cream races that has been involved in such crosses.

NILSSON (77, 1929) observed a very simple case. In the race Apollo, characterized by yellow seeds, he observed spontaneous segregation into 3 yellow : 1 chamois (described as yellowish grey-white). The relation to the types described above can not be stated.

A type that must be different from those treated above was described by KOOIMAN (56, 1920). It yet has several characteristics in common with other ecru types. In the first place the outer appearance, a greyish or yellowish smoky white, combined with coloured strophio-lum and ring around the hilum. In the second place the circumstance that is may bear several factors cryptomerically. It appeared in the  $F_2$  and further generations of a cross between a white and a yellow-brown seeded variety.

In  $F_2$  the segregation was as follows:

146 non-buff coloured : 8 buff : 58 white, which points to a 15 : 1 scheme among coloured offspring. This may be explained by the assumption of a factor D for buff, and of two other chromogenous factors B and C, to either of which D is hypostatic. The consequence of this assumption is that in some  $F_3$  families segregation into coloured, non-buff and buff in a ratio 3 : 1 may be expected. Such segregations have been actually observed.

Most probably the same type has been observed by SIRKS (100, 1922, p. 118—124). In the offspring of a spontaneous hybrid between a yellow-brown race and most probably the Kievitsboon (a red mottled race), and also in a spontaneous cross between a lemon-coloured yellow bean with probably the same Kievitsboon, ecru coloured beans appeared in small numbers. According to SIRKS the segregation should be considered to be 63 : 1; at least it is 15 : 1.

The relation between the different buff types is uncertain. The types of SHAW and NORTON and of MIYAKE may be closely related, even fundamentally identical. If this should be the case there must, however, be a fundamental difference between the modifiers (used in the sense of SHAW and NORTON) in the american and the japanese races involved in the crosses. The ecru type of NILSSON is not determinable from the simple material. That of KOOIMAN and SIRKS seems to be certainly different from the other ones; it is not basic but hypostatic to perhaps all other colours.

#### 4. *The yellow-black series of seed coat pigments*

Especially with respect to this group of colours KRISTOFFERSON's (60, 1924) remark is worth notice: „As to the literature on the inheritance of seed coat colour it must be said that the mode of denominating the factors is in an annoying state of confusion. Different

writers use one and the same symbol for different factors, and other use different symbols for one and the same factor. The result is that almost the whole alphabet has been employed for the denomination of only a few factors. Furthermore, the identifying of the colour nuances referred to is very difficult. Papers on this subject are written in at least six different languages, and writers of the same language often use different denominations for the same nuance". There is, no doubt, much truth in this complaint and there is still another cause of confusion in that apparently identical nuances often behave differently in apparently comparable types of crosses. Furthermore the crosses carried out are in most cases of a rather complicate nature. Historically considered this has a logical foundation, as originally the white seed coat colour was considered to be *the* recessive condition of coloured, thus presenting an apparently excellent test material with which the colour-factors of differently coloured types might be easily analysed. Nearly all such crosses resulted in mottled offspring and moreover proved the latency of several factors in most white-seeded races.

As this mottling behaved in a peculiar way, the solution of this problem asked a good deal of attention, and the interrelation of the seed coat colours was more or less summarily considered. Thus in most early analyses we only find the main colour types (black, coffee-brown (seal-brown), orange-brown (orange-yellow) and sometimes yellow) mentioned.

Nevertheless in the elaborate protocols of the early crosses of TSCHERMAK (121, 1902; 122, 1904) a lot of different shades of several colours are mentioned. I will give one example of such a cross: white-seeded Wachsschwert  $\times$  orange-brown Non Plus Ultra. The  $F_1$  was black-mottled and showed in  $F_2$  a complicate segregation into mottled, self-coloured and white. Of self-colours the protocol reveals:

White; white tinged with yellow; white tinged with brown; reddish light yellow; yellowish pink tinged with violet; light brown; light yellow-brown; reddish light brown; light reddish brown tinged with greyish violet; chocolate; light ochre-brown and ochre-brown, tinged with green, with blue-green, with grey-green; grey-brown tinged with blue-green; dark reddish brown; dark brown tinged with greyish violet; violettish brown; greenish brown; black. Enough to show that the matter is difficult and complicated.

In order to be able to give an at least in some respects coherent representation of the factors responsible for the colours in this group, I may be allowed to give a short historical introduction. Such simple relations as that between dark brown and yellow-brown (EMERSON, 20, 1904) were soon observed. SHULL (98, 1908) supposes a mono-factorial difference between light yellow (apparently lemon-coloured) and orange-brown, and considered black to be epistatic to orange-brown. Here consequently the simple dominant series black → brown → yellow is suggested.

TSCHERMAK (123, 1912) gives an emendation of this series, adding violet to the colours mentioned. This series is to be read as follows:

$$ABC = \text{Black} \begin{cases} ABc = \text{Violet} \\ AbC = \text{Brown} \end{cases} \quad Abc = \text{Yellow}$$

LUNDBERG and ÅKERMAN (66, 1917) show that within the yellow-brown group several colours exist that are factorially related in a simple way.

$$CG = \text{Dark brown} \begin{cases} Cg = \text{Chocolate brown} \\ cG = \text{yellow-brown} \end{cases} \quad cg = \text{yellowish white}$$

SHAW and NORTON (95, 1918) have apparently neglected the more subtle nuances of which their material must have abounded. Within the yellow-black series they simply distinguish yellow (factor C), Coffee-brown (factor F) and black (factor G) with the dominance relation suggested by SHULL  $G \rightarrow F \rightarrow C$ . Besides they distinguish „a possible light brown or olive brown, designated by H”.

KOOIMAN (56, 1920) gives a scheme that is fundamentally different in several respects from the foregoing, in which all the colours of the yellow-black series are considered as establishing one simple series, or at least as one fundamental colour which may be modified by at least two determining factors. In KOOIMAN's scheme, however, three different chromogenous factors may, in cooperation with the groundfactor A (which by itself is not active) cause a coloured seed coat. These chromogenous factors are:

B. AB gives lemon-colour. In a homozygous condition (ABB) it causes self-colour, in a heterozygous condition the ever segregating type of mottling. In this respect it will be considered in a separate chapter. Furthermore B leaves a ring round the hilum unpigmented.

C. AC gives a yellow- or orange-brown colour of a rather uncertain

tinge and less intense than known from the type Non Plus Ultra. A ring round the hilum is coloured in a darker brown tint.

D. AD gives a smoky greyish or yellowish colour to the entire seed-coat, with the exception of a small ring round the hilum, which is dark brown.

The factors in different combinations allow to establish several natural groups, as may be seen from table 9.

TABLE 9.

A absent		A present or absent	Groundfactor A present								
			One or more chromogenous factors present								
chromogenous factors absent or present	All chromogenous factors absent	B present						B absent			
		C present			C absent			C present		D present or absent	
		D present or absent		D present		D absent		D present			
		BB	Bb	BB	Bb	BB	Bb	C absent	D present or absent	C absent	
<sup>b c d</sup> aBCD	Abcd	Hard colours, self-coloured with darker coloured ring around the hilum		Hard colours, mottled, darker coloured ring around the hilum		Soft colours, self-coloured with darker ring around the hilum		Soft colours, mottled, with darker ring around the hilum		Soft colours, self-coloured uncoloured ring around the hilum	
		ABB <sup>a</sup> CD		ABb <sup>d</sup> CD		ABBcD		ABb <sup>c</sup> D		ABBcd	
white	white	Hard colours, self-coloured with darker coloured ring around the hilum		Hard colours, mottled, darker coloured ring around the hilum		Soft colours, self-coloured with darker ring around the hilum		Soft colours, mottled with darker ring around the hilum		Soft colours, self-coloured uncoloured ring around the hilum	
		AbCD		Ab <sup>d</sup> CD		AbBcD		AbB <sup>c</sup> D		AbBcd	
Ia	Ib	IIa	IIb	IIIa	IIIb	IIIc	IIId	IV	V		
White group		Hard colour group		Soft colour group				Half-hard colour group		Ecru	

Of these groups I and V have been considered in previous chapters. The groups II, III and IV will be considered here in more details, first in their mutual relations, than with respect to the effect of colour intensifiers.

The groups may be described as follows:

II. Hard colour group. This one is represented by self-coloured as well as mottled types, always with darker coloured ring around the hilum. The colours are clear and intense with the orange-brown as displayed by *Non Plus Ultra* as its simplest representant, black as the other extreme.

III. Soft colour group, displaying a lot of shades ranging from lemon-colour to dark brownish grey, either self-coloured or mottled. The ring around the hilum may be uncoloured or dark brown.

IV. Half hard colour group. In this group the colours are much less intense than in group II, ranging from yellowish brown to dark red-brown, even near black, mostly flushed with a steel-coloured, bluish or violettish hue. Often the ventral side of the seed is much lighter coloured. The ring round the hilum is dark brown. Mottling does never occur in this colour group.

From the factorial constitution of the groups the following consequences will be apparent:

Mottled hard colour group types may segregate all other groups. Self-coloured ones, however can only segregate white and soft colours. Of the soft colour groups, IIIa can never segregate ecru beans; mottled types (IIIb), however, *must* segregate ecru. Of the half hard colour group those that are heterozygous for C and have D will segregate ecru in  $1/4$  of all coloured offspring. These consequences are considered in Table 10, which has been composed after the data, relating to a cross between a white and an orange-brown bean, described by KOORMAN (56, 1920). It is only shows which types have been segregated without actual numbers.

TABLE 10.  $F_3$ -OFFSPRING

This is in accordance with the hypothesis. With respect to the actual numbers it should be considered that most  $F_2$  groups consist of several genotypes and that consequently most group-numbers will not show simple ratios. In some cases matters are simple. Thus all mottled soft-coloured types with coloured hilum-ring (ABbcD) gave together 133 soft-coloured mottled, 70 soft-coloured self (both groups with or without col. hilum ring): 48 ecru : 74 white. Here the ecru type is segregated in too small numbers, for among coloured types the ratio should have been 2 : 1 : 1 (125.5 : 62.75 : 62.75).

Further: all half-hard  $F_3$  families taken together consisted of 331 half hard : 55 ecru : 95 white, and leaving out the families that did not segregate ecru at all, as being most probably homozygous for C or D, we find 185 half hard : 55 ecru : 50 white. Here the deficiency of ecru is not significant (expected 180 : 60).

In both cases the ecru type seems to have been segregated according to a 3 : 1 ratio. In most  $F_3$  families and in  $F_2$  (hard-coloured mottled) it is segregated according to 15 : 1. Thus in  $F_2$  we find several coloured types 146 : 8 ecru (expected 144 : 10).

We have seen that all Bcd types have an uncoloured ring around the hilum. This implies that in  $F_2$  such types should be present in 3/63 of all coloured types. Actually found 12 out of 154 (expected 7.3). Among  $F_3$  families several ratios may be expected (3 : 1; 4 : 1; 15 : 1; 20 : 1).

The 3 : 1 ratio is found in group IIIa (especially from ABBcDd). Here the actual numbers are: 73 coloured hilum ring : 24 uncoloured one. The 4 : 1 ratio is found in group IIIb (especially from ABbcDd). Actual numbers 107 : 24 (expected 105 : 26). The ratios 15 : 1 and (or) 20 : 1 are surely represented among  $F_3$  families; these families are however too small in numbers to allow for other than a statistical proof.

Generally speaking and though in many details requiring corroboration, the hypothesis, advanced above, may be considered to be sufficiently founded. Yet the reviewer is well aware that it does by no means pretend to cover all facts reported by other investigators. Even with respect to the material that furnished the foundation of the hypothesis, complications such as coupling are not absolutely out of consideration.

With the exception of the ecru type, that is not changed to any

TABLE 11.

Scheme I				Scheme II			
	BCEF	BCEf	BCEF	BCEF	BCEf	BCEf	BCEf
	Black	Coffee-brown	Violet-brown	Orange-brown	Black	Coffee-brown	Orange-brown
BBCC <del>EE</del> FF	Black	constant	—	—	constant	—	—
BBCC <del>EE</del> FF	Black	3	1	—	3	1	—
BBCC <del>E</del> FF	Black	3	—	—	constant	—	—
BBCC <del>E</del> Ff	Black	9	3	.1	12	3	1
BBCC <del>E</del> Ff	Coffee-brown	—	constant	—	—	constant	—
BBCC <del>E</del> ff	Coffee-brown	—	3	—	1	3	1
BBCC <del>E</del> ff	Violet-brown	—	—	constant	—	—	—
BBCC <del>E</del> Ff	Violet-brown	—	—	3	1	3	1
BBCC <del>E</del> ff	Orange-brown	—	—	—	constant	—	—

considerable extent, all other colour groups comprise a number of different colours resulting from the action of additional factors (determiners of SHAW and NORTON, intensifiers of KOOIMAN). With respect to these intensifiers we may say that they are inactive save in collaboration with the groundfactor and at least one of the chromogenous factors B and C. As to their number and interrelation there is yet no common opinion. In some cases black seems to be a simply dominant over coffee-brown, coffee-brown over orange-brown; in other cases black appears to be dominant over coffee-brown and violet-brown, both latter colours over orange-brown. The different consequences of both constellations may be seen from a comparison of the following two simple cases. In these cases B and C are chromogenous factors in the sense advanced above; In Case I BC cause an orange-brown colour, E changes orange-brown into coffee-brown, F changes orange-brown into violet-brown, EF change BC into black. In case II E causes the dark coffee-brown, F either with or without E black. (See Table 11).

The difference between both schemes is apparently that with some genotypes the additional action of factor F in case I causes violet, in case II black.

As only KOOIMAN distinguishes between principal colour groups within the yellow-black series, we can only give his opinion of the effect of the factors E and F in these groups.

TABLE 12.

Modifying factors series ↓	→ No modifiers	Ef	eF	EF
Bc. Soft colours	lemon-colour	soft brown	pale grey	dark grey
bC. Half-hard colours	sallow orange- brown	grey-brown	reddish violet brown	dark red- brown with violet tinge
BC. Hard colours	orange-brown	coffee-brown	violet-brown	black

Table 13 gives a survey of all segregations which form the consequence of the described interaction of these four factors, with the proviso that of all B-offspring of mottled types  $\frac{1}{3}$  are mottled,  $\frac{2}{3}$  self-coloured, and besides that the coloured : white segregation is left out of consideration.

TABLE 13.

Number of segregation type	Genotype of segregating plant	Genotype of segregants	Phenotype of segregants			BCEF	bCEF	bCef	BcEf	BcEf	bCef	Sallow Yellow							
			Phenotype of segregating plants																
			Black	Reddish-brown tinged w. violet	Half-hard brown														
1	BBCCEEFF	Black	c	Coffee-brown	Black	BCEF	BCEF	BCEF	BCEF	BCEF	BCEF	Sallow Yellow							
2	BBCCEEFf	"	9 3 3	1	"	BCef	BCef	BCef	BCef	BCef	BCef								
3	BBCCEe FF	"	9 3 3	1	"	Orange-brown	Orange-brown	Orange-brown	Orange-brown	Orange-brown	Orange-brown								
4	BBCCEe Ff	"	9 3 3	1	"	Dark grey													
5	BBCCEEff	Coffee-brown	c	"	"	Soft brown													
6	BBCCEe ff	"	3	"	"	Light grey													
7	BBCCee FF	Violet-brown	c	"	"	Lemon-coloured	Lemon-coloured	Lemon-coloured	Lemon-coloured	Lemon-coloured	Lemon-coloured								
8	BBCCee Ff	"	3	"	"	Reddish-brown	Reddish-brown	Reddish-brown	Reddish-brown	Reddish-brown	Reddish-brown								
9	BBCCee ff	Orange-brown	c	"	"	tinged w. violet													
10	BBCc EEFF	Black	3	"	"	Half-hard brown													
11	BBCc EEFf	"	9 3	"	"														
12	BBCc Ee FF	"	9	"	"														
13	BBCc Ee Ff	"	27	9 9 3	9 9 3	1	1	1	1	1	1								
14	BBCc EEff	Coffee-brown	3	"	"														
15	BBCc Ee ff	"	9	3	3	3	3	3	3	3	3								
16	BBCc ee ff	Violet-brown	3	"	"														
17	BBCc ee Ff	"	9	3	3	1	1	1	1	1	1								
18	BBCc ee ff	Orange-brown	3	"	"														
19	Bb CCEEFF	Black (mottled)	3	"	"														
20	Bb CCEEFf	"	9 3	"	"	1	1	1	1	1	1								
21	Bb CCEe FF	"	9	3	3	3	3	3	3	3	3								
22	Bb CCEe Ff	"	27	9 9 3	9 9 3	3	3	3	3	3	3								
23	Bb CCEEff	Coffee-brown	3	"	"														
24	Bb CCEe ff	"	9	3	3	3	3	3	3	3	3								
25	Bb CCee FF	Violet-brown	3	"	"														
26	Bb CCee Ff	"	9	3	3	1	1	1	1	1	1								
27	Bb CC ee ff	Orange-brown	3	"	"														
28	Bb Cc EEFF	Black	9	"	"														
29	Bb Cc EEFf	"	27	9	9	3	3	3	3	3	3								
30	Bb Cc Ee Ff	"	27	9	27	9	9	9	9	9	9								
31	Bb Cc Ee Ff	"	81 27 27	9 27	9 27	9	9	9	9	9	9								
32	Bb Cc EEff	Coffee-brown	9	"	"	3	3	3	3	3	3								

Number of segregation type	Genotype of segregating plant	Genotype of segregants	Phenotype of segregants										
			Phenotype of segregating plants					Phenotype of segregants					
			Black	Coffee-brown	Violet-brown	Orange-brown	Dark grey	Soft brown	Light grey	Lemon-coloured	Reddish-brown tinged w. violet	Half-hard brown	
33	Bb Cc Ee ff	Coffee-brown (mottled)	27	9	9	3	3	9	3	3	9	3	
34	Bb Cc ee FF	Violet-brown "										3	3
35	Bb Cc ee Ff	" "	27	9	9	3	3	3	3	3	9	3	3
36	Bb Cc ee ff	Orange-brown,"											3
37	bb CCEEFF	Reddish br. ting- ed w. violet											
38	bb CCEEFFf	"							3	1			
39	bb CCEe FF	"							3	1			
40	bb CCEe Ff	"							9	3	3	1	1
41	bb CCEEff	Half-hard brown							c	c			
42	bb CCEe ff	"							3	3			1
43	bb CCee FF	Half-hard viol- brown								c	3		
44	bb CCee Ff	"								3	1		
45	bb CCee ff	Shallow yellow									c		
46	BBcc EEFF	Dark grey											
47	BBcc EEFf	"			3	1	1						
48	BBcc Ee FF	"			3	1	1						
49	BBcc Ee Ff	"			9	3	3	1					
50	BBcc EEff	Soft brown			c	c	3	1					
51	BBcc Ee ff	"			3	c	3	1					
52	BBcc ee FF	Light grey					c	3	1				
53	BBcc ee Ff	"						3	1				
54	BBcc ee ff	Lemon-coloured							c				
55	Bb cc EEFF	Dark grey (mott- led)											
56	Bb cc EEFf	" "				3	1						
57	Bb cc Ee FF	" "				3	1						
58	Bb cc Ee Ff	" "				9	3	3	1				
59	Bb cc EEff	Soft-brown				c	3	1					
60	Bb cc Ee ff	" "					3	c	1				
61	Bb cc ee FF	Light grey						c	3	1			
62	Bb cc ee Ff	" "							3	1			
63	Bb cc ee ff	Lemon-coloured,,							c				

Both groups of soft colours 46—54 and 55—63 behave in a similar way (mottling left out of consideration). Crosses between soft-coloured types have not come to my attention; segregations that fall into this<sup>c</sup> class have, however, been observed. Thus KOOIMAN (56, 1920) and LUNDBERG and ÅKERMAN (1917) report the following segregations from extracted soft-coloured types.

TABLE 14.

Segregating type	Scheme Nr. Table 13	dark grey	light grey	Soft-brown „choklad- färgade”	lemon-col. „gulvita”	Author
Among F <sub>2</sub> plants		22	6	11	3	KOOIMAN.
F <sub>2</sub> dark grey . . .	49	81	17	19	4	"
dark grey . . .	47	51	22	—	—	"
light grey . . .	53	—	15	—	3	"
soft brown . . .	51	—	—	20	5	"
chokladfärgade	51	—	—	70	26	LUNDBERG & ÅKERMAN.

Besides all these colours occasionally breed true.

SIRKS' cross 13, (100, 1922) Lemon-coloured × white? certainly belongs here. The numbers are, however, too small to be of much value.

In the cases reviewed in Table 15 the material bearing upon the interrelation of the soft and hard colour groups is brought together.

TABLE 15.

Segregating type	Scheme Nr. Table 13	dark brown	orange- brown	soft brown	lemon- coloured	Author.
Dark brown . . .	15	47	27	24	14	LUNDBERG & ÅKER- MAN.
" . . .	6	127	48	—	—	"
" . . .	14	316	—	121	—	"
Orange-brown . .	18	—	216	—	89	
" . . .	18	—	382	—	130	SHULL 1908, p. 445.
" . . .	18	—	48	—	16	SIRKS 1922, p. 112.

The data borrowed from LUNDBERG and ÅKERMAN are obtained by the addition of several segregating families.

The factorial analysis of these cases gives us an opportunity to identify some of the factors.

LUNDBERG & ÅKERMAN . . . . .	G	C
SIRKS . . . . .	G	
SHULL . . . . .	Y	O
KOOIMAN . . . . .	B	C E

The interrelation between the other groups of Kooiman's scheme is in no case clear, as such groups have nowhere else been considered. Some cases however apparently belong to the group of hard colours. They are brought together in table 16.

TABLE 16.

Cross	Author	F <sub>2</sub> resp. F <sub>3</sub> segregation	Scheme Nr. of Table 13
Stringless green(dark brown) x Giant Stringless (yellow brown)	EMERSON, '04.	3 dark brown (resp. 1 dark brown + 2 medium dark brown) : 1 yellow brown	6 BCE x BCe
White Navy x Challenge Black Wax	"	13 black : 7 black mottled : 10 white; F <sub>3</sub> 30 black : 34 black mottled : 9 white	19? bCEF x BCEF
Prolific Black Wax x Ne plus ultra (imperfectly recorded)	SHULL, 1908.	174 black : 47 seal brown : 26 brown	4? BCEF x BCef
Prolific Black Wax x Yellow Six Weeks (imperfectly recorded)	"	155 black : 55 dark brown : 9 yellow dark brown, orange-brown and yellow probably mixed up	12 BCEF x Bcef
Spontaneous hybrid	TJEBBES and KOOIMAN 1919	Black + blue mottled 43 : brown + brownish purple mottled 9 : black 16 : brown 5 = black : brown = 59 : 14	2 constant mottling BCEFF (Mm)
Orange-brown x black	SIRKS 1922 cross 10	39 black : 6 dark reddish brown : 3 orange brown	?
Black x yellow	MIYAKE a. o. 1930	121 black : 39 brown : 11 yellow	?
Dull greyish brown x black	"	103 black : 34 brown : 10 greyish brown : 6 yellow	2 scheme perhaps 48 : 12 : 3 : 1

These data are not apt to give us a firm conviction that the problem is well on its way to be solved. Another serious difficulty may be added when considering more complicate crosses.

TSCHERMAK (123, 1912) gives a summary of his results in bean crosses. The material is more extensive than intensive. Nevertheless interesting data are produced.

Non Plus Ultra (orange-brown)  $\times$  Wachsschwert (white).  $F_1$  black mottled.  $F_2$  black mottled 92, violet mottled 33, brown-mottled 38, black selfcol. 39, violet selfcol. 27, brown selfcol. 101. This seems to be a most unexpected type of segregation. Among mottled types the segregation is apparently according to a 9 : 3 : 4 ratio, among self-coloured types the ratio seems to be reversed into 4 : 3 : 9. TSCHERMAK tries to account for this reversion by an absolutely unsatisfactory hypothesis of association and dissociation of factors.

KOOIMAN (56, 1920) ventured to propose another solution of this special case. From the schemes given in table 13 a more general solution may be derived. Those cases that may throw a light upon this problem are represented in table 17.

TABLE 17.

Scheme number of table 13	Black, mottled	Non-black, mottled	Black, self- coloured	Non-black, self-col.
20, 21	6	2	3	5
22	18	14	9	23
28	6	2	3	4
29	18	14	9	19
30	18	30	9	51
31	54	74	27	85

Now, if we suppose that TSCHERMAK's cross is to be considered as BCef  $\times$  bCEF (scheme number 22), than  $F_1 = BbCCeEfF$  and  $F_2$  should show the following segregation.

2 BbCC<sub>EF</sub><sup>ef</sup> (mottled) : 1 BBCC<sub>EF</sub><sup>ef</sup> (self) : 1 bbCC<sub>EF</sub><sup>ef</sup> (self).

The mottled group consists of:

9 black (BbCCEF) : 3 violet (BbCCeF) : 4 brown (BbCCEf + BbCCef). The group BBCC<sub>EF</sub><sup>ef</sup> (that is the hard-coloured group) shows the same segregation, the half-hard group (bbCC<sub>EF</sub><sup>ef</sup>) is sup-

posed to consist of violetish dark brown to sallow brown colours in a ratio of say 3 : 13. The addition of all self-coloured types results in the following ratio:

$$\begin{array}{r}
 9 \text{ black} : 3 \text{ violet} : 4 \text{ brown} \\
 3 \text{ violet} : 13 \text{ brown} \\
 \hline
 9 \qquad \qquad \qquad 6 \qquad \qquad \qquad 17
 \end{array}$$

As the distinction between brown and violet colours is often difficult we may test the observed black : non-black ratio to the hypothetical one. Theoretical 9 : 23; observed 39 : 128 = 7.5 : 24.5. This is, considering the abundance of colour types (cf. p. 340) and the consequently rather arbitrary classification, not at all an improbable solution.

The other crosses reported by TSCHERMAK have mostly too small numbers to be valuable for the present problem. Hundert für Eine  $\times$  Schwarze Neger gave in  $F_2$  57 black mottled : 35 mottled in other colours : 12 black selfcoloured : 63 other selfcoloured types. This is comparable to the former cross. In both cases blacks appear in such numbers that the schemes seem to be related to the 9 : 7 (or 3 + 4 or 3 + 3 + 1) rather than to the 12 : 3 : 1 ratio.

Also some crosses investigated by SIRKS (100, 1922) might be classed here. Thus in cross 12a = Orange-brown  $\times$  white,  $F_1$  black-mottled,  $F_2$ , consisting of several small families, 97 black mottled : 51 other mottled colours : 55 black self-coloured : 76 other self-colours; and cross 12b, where in  $F_2$  the same types are represented by the numbers 11, 4, 8 and 14.

In KOOIMAN's case the same „reversion” is found; if we leave out the soft-coloured class, the same  $F_2$  groups are found as in the cases considered above, in the following numbers: 26 : 20 : 11 : 44. If the soft-coloured types are not left out we find 26 black mottled, 49 other mottled types, 11 black self-coloured : 65 other self-coloured types, which points to a segregation according to schemes 30 or 31 of table 13.

|| In the scheme of table 13 it has been supposed that a 9 : 7 ratio is at the back of the black : brown-violet-yellow segregation. Of course a 12 : 4 ratio should give other derived ratios; yet the principle of reversion might hold good. This ratio is forwarded by SHULL (see

table 16), and seems to be also represented by the crosses of SIRKS and those of MIYAKE (same table).

This also might be true of the crosses by SHAW and NORTON, that however are not liable to a detailed analysis as the authors have not separately considered the colour segregation among mottled and self-coloured types.

Perhaps a very simple case is that described by NILSSON (77, 1929) who observed among orange-brown beans a segregation into 3 orange-brown : 1 more or less chamois type, described as greyish-yellowish white. If this type belongs to the soft colour group then the segregating plants might be considered to be BBCc.

Also a case observed by KRISTOFFERSON (60, 1924) seems rather simple. This experimenter found segregation from black-mottled types into 1 black : 2 black-mottled : 1 steel blue. Steel blue = steel-coloured on a brown back-ground, apparently a half-hard colour type. The genotype of the hybrid might consequently simply be Bb[CCEEFF]. KRISTOFFERSON advances an unnecessarily complicate solution, following SHAW and NORTON, and assumes as the hybrid genotype [PCG]  $\frac{K}{Y}$   $\frac{Y}{Z}$   $\frac{K}{Y}$   $\frac{Z}{Z}$ , in which K is a blackening factor, k representing the diluted condition seen in steel-blue.

TABLE 18.

Phenotype of offspring	Red-brown	Grey-brown		Orange-brown		Lemon-coloured		Scheme of segregation.
		col. hilum ring	white hilum ring	GdL	gDl	coloured hilum ring	white hilum ring	
Genotype of offspring	GdL	gDl	GdL	gDl	GdL	gDl	GdL	gdl
1. Citroen $\times$ Wagenaar . . . . .	—	—	—	—	99	30	gDl : gdl = 3 : 1	
2. Wagenaar $\times$ Orange-brown . .	—	—	—	240	77	—	3 : 1	
3. Citroen $\times$ Orange brown . . . . .	—	—	—	48	—	16	GdL : GdL (or gdl) = 3 : 1	
3a. id.	—	—	—	80	25	33	9 : 3 : 4 (GdL + gdl)	
4. Citroen $\times$ rotjes . . . . .	46	14	23	12	5	12	27 : 9 : 12 : 9 : 3 : 4	
5. Orange-brown $\times$ rotjes . . . . .	186	78	—	68	13	—	9 : 3 : 3 : 1.	

SIRKS (100, 1922) carried out a number of crosses between some apparently nearly related simple types: lemon-coloured with white hilum ring ("Citroen"), lemon-coloured with brown hilum ring (Wagenaar), Orange-brown bean (Non Plus Ultra type), and a dark brown type ("Rotjes"). Among the offspring in many cases several slightly different shades of reddish and greyish brown have been distinguished. In the table 18, p. 353, the data have been rendered in a simplified way the distinction of shades having been left out of consideration.

SIRKS supposes that factor G is identical to KOOIMAN's C, D is identical to D, whereas L might be E. Further it is assumed that G is only active in the presence of D. In the opinion of the reviewer it is at present impossible to explain the apparent inconsistency between the experiments of both authors.

##### 5. *The red colour series.*

It is not questionable that not every colour type denominated in literature as red, blue, purple etc., names that clearly seem to indicate a relation to the red colour group, really belongs here. Purple sometimes is a purplish brown or even a deep bluish black and in such cases is of the yellow-black parentage; sometimes it is a clear violet of rather uncertain parentage or a purplish red of doubtless red origin. Such differences may perhaps account for many apparently irreconcilable observations.

There are only very few observations of crosses between races that undoubtedly belong to the red colour series. In a cross by SHAW and NORTON between a light red (Red Valentine) and a dark (purplish) red variety (Keeney Rustless), dark red is said to behave as a simple dominant. In crosses of Blue Pod Butter with light red varieties  $F_1$  is sometimes recorded as light red, sometimes as dark red, yet in all cases we find segregation into dark red, light red and buff (ecru). The classification seems to be difficult; apparently dark reds or intermediates have been classed as light red. SHAW and NORTON denominate the light red factor as D, which is influenced by the dark red factor E. Blue Pod Butter, when crossed with dark red varieties gives dark red in  $F_1$  and segregation in dark red, light red and buff in  $F_2$ . From this we might conclude that in all crosses with light reds, Blue Pod Butter is factorially to be considered as carrying factor E, in all crosses with dark reds it should have been e. This seems rather improbable.

TJEBBES and KOOIMAN (115, 1921) observed a spontaneous hybrid of the pole Cranberry bean in which apparently only red colours are involved. In this case the following factors may be supposed to be involved:

R the chromogenous factor of the red series.

Bl a factor that changes red colours into bluish ones.

Z and (or) Z' which intensify and blacken the colours.

These factors, through interaction, produced the following colours:

Black	RR Bl $\underbrace{\text{bl}}_{\text{Bl}} Z_z^z$
Bluish grey	Rr Bl $\underbrace{\text{bl}}_{\text{Bl}} Z_z^z$
purple	RR Bl $\underbrace{\text{bl}}_{\text{Bl}} zz$
violet	Rr Bl $\underbrace{\text{bl}}_{\text{Bl}} zz$
Brownish black	RR bl bl $\underbrace{Z_z^z}$
Reddish grey	Rr bl bl $\underbrace{Z_z^z}$
Red	RR bl bl $\underbrace{zz}$
Pale red	Rr bl bl $\underbrace{zz}$

#### *The interrelation of yellow-black and red colours*

This is an unsolved and extremely difficult problem. From the work of SHAW and NORTON (95, 1918) we may get the general impression that the hypothetical "modifiers" are absolutely linked, which leads in cases of crosses between yellow-black and red types to absolute repulsion. TJEBBES and KOOIMAN (113, 115) have deducted from such a cross a repulsion between the Red-factor R and especially one of the chromogenous factors of the yellow-black group, to wit B. As B and C are freely segregating R and C cannot be linked. Whether this might explain certain observations of cases in which yellow-black factors and red factors are not linked must be left unanswered. It is only advanced as a working hypothesis.

As a matter of fact we may observe two sharply distinct groups of observations: 1. Those in which red simply seems to form a member of the yellow-black series; 2. those in which red and yellow-black show absolute repulsion; if both are present, they are present in a heterozygous condition.

*Group I.*

With certainty only a few crosses by MIYAKE a.o. (75, 1930) belong here.

1. Cream  $\times$  white.  $F_1$  reddish purple;  $F_2$  30 reddish purple, 6 purple, 2 red, 19 cream, 18 white.

2. Purple mottled  $\times$  cream.  $F_1$  brownish mottled;  $F_2$  69 brownish mottled; 23 purple mottled, 8 red mottled, 6 yellow mottled, 47 cream.

3. Red  $\times$  black;  $F_1$  black;  $F_2$  184 black, 107 brown-yellow, 21 red, 26 grey (described and pictured as a dull greyish brown).

The authors give only very summarily a few indications as to an analysis of these segregations. The reviewer may be allowed to attempt a solution.

Case 1. Coloured : white = 3 : 1; among coloured beans cream is apparently segregated in a 1 : 3 ratio; among coloured-non-cream we might suggest 12 reddish purple : 3 purple : 1 red.

Case 2. We may assume that cream is segregated according to 3 : 1, though there is a marked surplus (less than 2 σ) of creams. If this is not considered to be significant we might suggest, if we are allowed to take brownish and yellow together, the following segregation:

9 brownish-yellow : 3 purple : 1 red : 4 cream  
(75) id. (23) id. (8) id. (47) id.

Case 3. With red as a double recessive and taking brown-yellow and grey together, we may assume the following segregation:

9 black : 6 brown-yellow-grey : 1 red.

In all these cases red seems to behave as a simple recessive to either the simplest representative of the brown series or to purple and more or less closely as a double recessive to the  $F_1$  types. It should be further kept in mind that in cases 1 and 3 *no mottling is brought about and that in case 2 no mention is made of double mottling*.

SIRKS observed some cases that may be best considered here though their bearing is not at all clear.

This experimenter (99, 1920) observed the segregation of a spontaneous hybrid of a race of Kievits-beans, in this paper described as a striped race, striping violet upon a chamois ground colour. The hybrid was striped leaden blue upon a liver-coloured ground-colour. The segregation may be schematically rendered as follows:

Self-coloured. 1 chamois, 15 yellow-brown to bluish brown.  
 Striped. 4 chamois with violet or grey stripes, 24 several solid-coloured ground colours with violet, grey or blue stripes. 9 mottled backgrounds with violet or blue stripes.

White 24.

Of all these plants offspring was grown. The results are analysed with the assumption of 7 factors of which one is S, the factor for striping. This is assumed to restrict blue, violet and grey pigments to stripes. If the background is grey or violet it is changed into mottling by S.

We may consider the denomination of the colour of the Kievits-bean as violet inadequate. In an other publication it is more correctly described as reddish violet and as a matter of fact it most probably belongs to the red colour series.

The segregation is too complicate, the identity of the factors too uncertain to successfully attempt the inclusion of this case in a general consideration. Perhaps, however it is more or less related to the following cases. It has, however, one remarkable feature that is not observed in the latter, the mottled background, that apparently belongs to the true-breeding type.

In the other cases, described by SIRKS (100, 1922) the Kievitsboon is described and figured as a mottled type, mottling reddish violet upon chamois. The data have been arranged in the following table. (Table 19, page 358).

Interesting in these cases is the absence of double mottling, which distinguishes them from the crosses to be treated next. Apparently the factor for reddish violet (K after Sirks) is simply one of a series of determiners in which undoubtedly yellow-black factors have a part. We may conclude this consideration by a description of the factorial solution by SIRKS.

Factors.

- A causing lemon-colour
- G yellow-brown (orange-brown)
- D dark ring round the hilum
- K (provisional) causing violet striping
- Bl changing reddish violet into blue-violet
- L factor for liver-colour
- Z factor for black colour.

Kievits . . . . . b g K D . bl z

Citroen . . . . .	BB	g <sup>k</sup>	k	d	. . .
Orange-brown . . .	<sup>b</sup> B	G	k	D	l bl z
Wagenaar . . . . .	B	g	k	D	. . .
Rotjes . . . . .	B	G	k	D	L Bl .
Black . . . . .		G	k	L	Bl Z

TABLE 19.

Cross									
Citroen × Kievits . .	106	39	15	11	37	—	—	—	2
Orange-br. × Kievits	92	43	11	28	17	—	—	—	1
Rotjes × Kievits . .	26	15	12	9	35	—	—	—	
Kievits × Black? . .	28	1	2	6	1	—	—	—	

## Group 2.

TSCHERMAK (123, 1912) described two crosses that may be of interest here as an introduction. The generations, however, are too small in numbers to be of fundamental importance.

1. Non plus ultra, yellow-brown × Weisse Ilsenburger.  $F_1$  Violet-brown mottled (also: light- and dark-brown mottled, flushed with violet near the hilum).  $F_2$  2 violet-brown mottled, 1 violet + brown double mottling, 1 brown mottled, 1 red mottled, 2 brownish violet self-coloured, 5 white.

2. Flageolet, purple mottled  $\times$  Black Wax.  $F_1$  black and violet mottled.  $F_2$  simple mottling: 2 black, 5 violet, 1 red; double mottling: 3 black + violet, 2 violet + brown, 1 red + brown; self coloured: 3 black, 2 ochre brown, 1 yellow.

The one thing that is extremely interesting besides the appearance of red, violet, black and brown among the offspring is the double mottling. It should be observed that Non Plus Ultra as well as Black Wax belong to the hard colour type, characterized, according to the opinion of the reviewer by the BC factor combination of which B is assumed to cause mottling in the heterozygous condition.

A case of double mottling, or rather of mottling and striping is also described by KAJANUS (51, 1914) in a spontaneous hybrid. Here, however, all offspring are either mottled, striped, or mottled and striped, the colours ranging from reddish yellow to violet. Most probably this case does not bear upon the present problem.

SHAW and NORTON (95, 1918) present material that undoubtedly is of prime importance. We only can regret that the presentation and analysis of the data is not equal to their importance. I may be allowed to represent their table XX. (See page 360).

This table, however, needs some comments. In the first place it is stated that all  $F_1$  beans of these crosses are double mottled, usually showing the colours of the red as well as of the yellow-black series. The yellow-black  $F_2$ — $F_4$  beans are partly mottled and partly self-coloured. The mottled ones never breed true to mottling. All yellow-black types, however breed true to these colours. All yellow-black + red mottled beans break up exactly like the  $F_1$  generation. Solid red beans do not appear and all red mottled ones breed true, though buff may be segregated.

With respect to the segregation of buff beans the record is not clear. It is stated that in the crosses 3, 7, 10, 12, 13 and 15 buff beans appear in small numbers in  $F_3$  and  $F_4$ , none having been observed in  $F_2$ . "In the other crosses more have been observed. If the parent varieties possess a determiner in common the chances of a buff bean appearing would be small". It has been stated before that SHAW and NORTON assume two modifiers M and M' for the yellow-black and red series. From crosses in which M and M' are heterozygously involved we might expect 1 buff : 15 other colours. It consequently is to be regretted that actual numbers of buff beans are not mentioned.

TABLE 20 after SHAW and NORTON

Parent Varieties	F <sub>2</sub>			F <sub>3</sub> and F <sub>4</sub>				y — b parents	y — b parents
				y — b + r parents		r			
	y — b	y — b + r	r	y — b	y — b + r	r	y — b	r	
1. Golden Eyed Wax (y-b) × Red Valentine (r) . . . . .	—	—	—	12	16	16	80		
2. reciprocal cross . . . . .	12	36	15	8	12	6	—		
3. Red Valentine (r) × Giant stringless (y-b) . . . . .	5	20	10	18	41	4	41		
4. Burpee Stringless (y-b) × Red Valentine (r) . . . . .	—	—	—	20	11	7	25		
5. reciprocal cross . . . . .	20	55	8	25	44	16	102	72	
				12		29			
				13	17				
6. Red Valentine (r) × Prolific Black Wax (y-b) . . . . .	10	15	5	10	9	10	202	15	
7. Currie (y-b) × Red Valentine (r) . . . . .	21	36	17	11		11		76	
8. Challenge Black Wax (y-b) × Warwick (r) . . . . .	13	14	2	3	7	2			
9. Giant Stringless (y-b) × Wardwell (r) . . . . .	20	33	11	23	32	8	117	26	
				11	14				
				13	6				
				7					
10. Giant Stringless (y-b) × Keeney Rustless (r) . . . . .	1	3	1	9	18	9	36	5	
11. Giant Stringless (y-b) × Mohawk (r) . . . . .	2	6	6	17	4	1			
12. Mohawk (r) × Giant Stringless (y-b) . . . . .	2	5	8	27	49	13		37	
13. Currie (y-b) × Mohawk (r)	49	90	32	11	10	6	85	15	
				16		6			
				15	10				
14. Mohawk (r) × Currie (y-b)	8	19	9	2	11	2	24	8	
15. Keeney Rustless (r) × Burpee Stringless (y-b) . . . . .	3	6	2	7	11	3	30	25	

What interests us most in these data may be stressed in the following points.:

1. the segregation into mainly three group in a 1 : 2 : 1 ratio.
2. the double mottling in the largest group.
3. the presence of inconstant self-coloured and mottled types among the yellow-black group.
4. the appearance of small numbers of buffs.

SHAW and NORTON assume that the crosses, represented in their table XX may be expressed by  $YZmM' \times yZMm'$  in which Y and Z are mottling factors M and M' the yellow-black and red modifiers. Now as Y and Z are absolutely linked and, according to the authors both modifiers are associated with one of the mottling factors we may conclude that the cross, in their line of thought should have been presented by  $YZmM' \times yZMm'$ . This would lead to a simple  $F_2$  scheme 1  $YZmM'$   $YZmM'$  : 2  $YZmM'$   $yZMm'$  : 1  $yZMm'$   $yZMm'$ . As however small numbers of buff beans appear, this scheme is too simple. If we take into account a red and a yellow-black determiner and represent for shortness sake  $YZmM'$  by O,  $yZMm'$  by o, then we get, from  $OoRrBb$  the following segregation

$F_2$  12  $OO_B^bR$ : 4  $OO_B^bR$ : 6  $OoBr$ : 18  $OoBR$ : 6  $OobR$ : 2  $Oobr$ : 12  $ooB_R^r$ : 4  $oobB_R^r$ .

If B is active only with o (M), R only with O (M') then we get

12	Brown self coloured	$(ooB_R^r)$
6	Brown mottled	$(OoBr)$
18	Brown + red mottled	$(OoBR)$
18	Red mottled	$(OO_B^bR + OobR)$
10	buff	$(OO_B^bR + Oobr + oobR)$

We thus find the phenotypes which were present in the  $F_2$  families, but in entirely different relations (18 : 18 : 18 : 10 instead of the actual (combined) data of table 20, 166 : 338 : 126 : ?).

We shall not attempt to find an auxiliary hypothesis to account for this deviation, as the assumption itself, in reviewers opinion, is of questionable value. We may, however point to one circumstance of foremost interest: if the mottling theory of EMERSON, to which SHAW and NORTON adhere, holds good, the segregated brown mottled types, when crossed with red self-coloured types, should produce constant red mottling.

KRISTOFFERSON (60, 1924) also describes a case of double mottling in which colours of the red and of the yellow-black series are simultaneously displayed. His material was derived from a spontaneous hybrid of brown beans. This double mottled type segregated into 48 double mottled : 7 violet mottled : 7 brown self-coloured : 3 yellowish white. The offspring of these plants is recorded in the following table.

TABLE 21.

SEGREGATION IN  $D_3$ 

The seed colour of $D_2$ plants	Genetical formula of the $D_2$ plants	Number of plants in $D_2$	$D_3$		
			Double mottled	Mottled	Self-coloured
			Brown	Yellowish white	
1. Double mottled . . .	BB DD YY ZZ	15	175	—	—
2. id. . .	Bb Dd Yy ZZ	10	71	18	16
3. id. . .	Bb DD YY ZZ	4	30	11	—
4. id. . .	BB Dd Yy ZZ	8	77	—	31
5. Violet Mottled . . .	bb DD YY ZZ	4	—	64	—
6. id. . .	bb Dd Yy ZZ	3	—	35	13
7. Brown self-coloured	BB dd yy ZZ	3	—	—	63
8. id.	Bb dd yy ZZ	3	—	—	30
9. Yellowish white . . .	bb dd yy ZZ	3	—	—	56

Here B is a factor for brown colour, D for violet, Y and Z are mottling factors. The double mottling as indicated in the table is not in all cases actually double mottling. "When all the factors B, D and Y are present in a heterozygous state the seed coat becomes distinctly double mottled". "When all factors are homozygous the violet colour seems to run together with the brown and the seed appears to be mottled in brown violet on a yellowish white ground. Individuals heterozygous in the brown factor B and homozygous in the factor group DYZ are of the same appearance". The representation of the facts in the above table is not very satisfactory. The number of individuals per family is very small, in group 1 about 12, in group 2 it is 11

in group 3 about 10, in group 4 about 13 and so on. This makes a trustworthy analysis of this case, that seems to deviate in a remarkable degree from other observations quite illusive. Thus group 1 is not really double mottled but actually simply violet-brown mottled, Equally group 3 is not really double mottled. In the column D3 double mottled such pseudo "double mottled" types are represented together with the real ones. If we count groups 2 and 4 together we find 148 "double mottled", 18 violet mottled, 47 brown, 7 yellowish white. Yellowish white is not described and might as well be chamois as lemon-colour. From a further table we see that of the 148 "double mottled" types 40 are recorded as brown-violet mottled. If we account for these we may group the numbers as follows

Group 2 + 4. 58 violet + violet-brown mottled : 108 double mottled : 47 (+ 7?) self coloured. This would lead to quite another solution.

Yet, though it might seem that this consideration is only presented to show the effect of "l'art de grouper les chiffres" we are willing to admit that KRISTOFFERSON's analysis may be to a certain extent correct and though he may not be able to prove his point, still it might present a possibility to reconcile these results with those of TJEBBES and KOOIMAN (113, 1919; 115, 1921) who found in a cross between an orange-brown bean and a red striped (Kievits) bean double mottling in  $F_1$ , segregation, in  $F_2$  into 1 kievits : 2 double mottled : 1 orange-brown.

#### COLOUR PATTERNS IN *Phaseolus vulgaris*

##### *Mottling*

The mottling of the seed coat consists in a more or less irregular pattern of a darker colour on a white or solid ground colour of yellowish to violet tinge. At least two patterns of true breeding mottling have been distinguished in genetical research, though no doubt more types are realised in established races. SHAW and NORTON have considered light and dark mottling, the latter behaving as a simple dominant to the former, whereas many other investigators distinguish mottling and striping. Dark mottling and striping may be combined with the eyed character, a centring of the pigment about the hilum,

which leaves a greater or smaller part of the seed-coat white or tinged in lighter colour. Besides the true breeding mottling an-ever-segregating type of mottling is well-known. As both types of mottling are generally considered to be caused by the same factors, these types are treated together.

### *Theories of Mottling*

The fact that mottling may exist as a constant racial character, side by side with a type of mottling that does not breed true and consequently has a heterozygous character, has given rise to several hypotheses; it is most remarkable that at the present time, nearly 30 years after the problem was first considered, a decision is not possible or at least not generally accepted.

TSCHERMAK (1901 and later) observed the novum that mottled beans were obtained in the cross of a white and a self-coloured race and suggested the cryptomeric presence of a mottling factor in the self-coloured race. In apparent agreement herewith is the fact (TSCHERMAK 122, 1904) that the  $F_1$  of the self-coloured races Schwarze Neger  $\times$  Hundert für Eine was also mottled. EMERSON (20, 1904) seems originally to have considered mottling as the heterozygous form of the black pigmentation, in his cross of Navy (white) and Challenge Black. SHULL (97, 1907) originally came to a hypothesis resembling that of TSCHERMAK, only considered the mottling factor (M) to be latent in the white seeded parent.

The equality in numbers of self-coloured and mottled progeny of mottled-seeded first generation plants, together with the fact that no single mottled bred true was soon found (TSCHERMAK 121, 1902; EMERSON 20, 1904; SHULL 97, 1907). SHULL (98, 1909) concluded from these facts that a mottling factor M, when present in a heterozygous condition only, causes mottling. In white as well as in self-coloured types it was supposed to be latent. If P is the Pigment factor, M the mottling factor we get the following scheme:

3  $P_B^P$  MM = self-coloured

6  $P_B^P$  Mm = mottled

3  $P_B^P$  mm = self-coloured

4  $pp^m_M$  = white.

This leads to the classical segregation scheme in case of inconstant

mottling, 6 mottled : 6 self-coloured : 4 white. As SHULL remarks, the relation between constant (racial) and ever-segregating mottling presents an interesting problem.

This problem was first taken up by EMERSON (21, 1909) in a paper in which he proposed two different factors, M causing the mottling that breeds true, X the sort that is ever-segregating, this factor only being active in a heterozygous condition. This hypothesis covered all the facts then known. As by these assumptions a relation between the two types is non-existent, EMERSON, not being satisfied, advanced in the same year (22, 1909) another theory, suggested to him by SPILLMAN in personal correspondence. This hypothesis suggests two factor pairs  $Yy$  and  $Zz$  that are absolutely linked. The factor combination  $YZ$  stands for true breeding mottling, the factor combinations  $Yz$  and  $yZ$  can only cause mottling if simultaneously present in the zygote and then cause the ever-segregating mottling. Consequently these combinations may be latent in white and self-coloured types.

SPILLMAN (104, 1911) gives the same hypothesis in a somewhat different formulation. He suggests that a mottling factor causes the production of two substances, a and c, that cooperate to realise mottling. This factor is represented by  $M_c^a$ . He furthermore assumes that in some races this factor has lost the faculty to produce substance a, thus changing into  $M_c^c$ ; in other races the faculty to produce c is supposed to have been lost, the mottling factor changing into  $M_a^a$ . This formulation certainly cannot be preferred to that by EMERSON.

This hypothesis of EMERSON-SPILLMAN is, however, not essentially different from a multiple allelomorph hypothesis, and as long as the observation of crossing-over does not prove this bifactorial scheme, we might represent the  $YZ$ ,  $Yz$ ,  $yZ$  and  $yz$  combinations more simply by M,  $M'$ ,  $M''$  and m. It should furthermore be remarked that such  $yz$  forms have never been used in crosses; it might be an interesting point to look out for a type that when crossed with either a  $Yz$  race and a  $yZ$  race does not produce ever-segregating mottling.

Although EMERSON's hypothesis was known to TSCHERMAK, this author (123, 1912) advanced another hypothesis that is rather too artificial and has, I believe, nowhere met with much approval. He proposes A as a basic factor for pigmentation, M as a mottling factor and suggests that mottling is due to the association = interaction of

the factors A and M. In cases of ever-segregating mottling this association is supposed to be induced by the heterozygous condition. In some self-coloured races M may be present in a homozygous condition. In such cases A and M are called dissociated ( $AA \downarrow MM$ ). In cases of true-breeding mottling the association  $\widehat{AM}$  is supposed in the heterozygous as well as in the homozygous condition. This hypothesis need not be critically considered. As to the nature of the factor M, TSCHERMAK considered it to be a local inhibitor. PLATE (81a, 1913) opposed to this opinion, considering M to be a factor that regulates the distribution of the pigment: in double dose, as MM, this distribution is regular over the entire seed coat (self-coloured types); in simple dose, as Mm, its action is weaker and mottling results. In cases of constant mottling the action is supposed to be still less effective.

The first suggestion that ever-segregating mottling might be considered as a consequence of the heterozygous condition of a pigmentation factor is found in EMERSON's early work (20, 1904). Here the hybrid between black and white was black mottled, segregating into black self-coloured, black mottled and white. EMERSON did not however seriously consider this possibility. KAJANUS (51, 1914) suggests the same explanation for the ever-segregating mottling, apparently because this would lead to a simpler factorial representation of the data and also on account of the absolutely hypothetical nature of the Y and Z factors. This hypothesis has been extensively considered and developed by KOOIMAN (56, 1920).

With respect to a full representation of the material we may refer to p. 341 sq. Here we may simply state that one of the chromogenous factors, B is supposed to cause mottling if present in a heterozygous condition. If all other factors save the groundfactor for colour A are present in their recessive condition the seed coat is lemon-coloured with uncoloured ring around the hilum, mottled if B is present in a heterozygous condition, self-coloured if the type is BB.

Of the several hypotheses presented only both EMERSON's and that of KOOIMAN seem worth while a closer consideration.

As the matter is of considerable theoretical interest a comparison of the postulates of both EMERSON's and of KOOIMAN's hypotheses may be given for a comparatively simple case. As a suitable material I have chosen the least complicate phenotypical group of  $F_2$  segregates in KOOIMAN's cross of orange-brown  $\times$  white bean (Bruine boon

× Dubbele Hollandsche Spersieboon). This group is phenotypically characterized by the soft colours, ranging from lemon-colour to dark brownish grey, and by an uncoloured ring around the hilum. The factors involved are

1. according to KOOIMAN's hypothesis

A groundfactor for pigmentation, not causing the production of pigment unless in cooperation with a chromogenous factor.  
B a chromogenous factor that causes mottling in the heterozygous condition.

2. According to Emerson's PXM hypothesis the factors P for pigmentation and X for inconstant mottling.

3. The same hypothesis may be amended by the assumption that P is only active in the presence of a groundfactor A.

4. According to EMERSON's YZ hypothesis, the factors P, Yz and yZ are involved. This may be amended by the same assumption as in case 3. We then get

5. factors A, P, Yz and yZ.

In the present case the consequences of 2 are identical to those of 4; equally 3 and 5 have identical consequences.

The comparison may therefore be restricted to cases 1, 2 and 3.  
(Table 22, see page 368).

This table reveals a striking difference between KOOIMAN's hypothesis on the one hand, both EMERSON's hypotheses on the other hand: In  $F_2$  as well as  $F_3$  the ratio of self-coloured and mottled in the first case is 1 : 2, in the other cases 1 : 1

Actually the data have been:

$F_2$  3 self-coloured and 9 mottled beans

the  $F_3$  of 9 mottled  $F_2$  plants gave the combined figures 46 mottled : 26 self-coloured. It may be further noted that among the offspring of other  $F_2$  types the ratio of mottled and self-coloured beans of the soft colour group is always equally 2 : 1 (Actual numbers 133 : 70; 72 : 36).

This is strongly in favour of KOOIMAN's hypothesis, though no doubt an auxiliary hypothesis to EMERSON's might be constructed to make it explain the facts.

In the above case the consequences of both EMERSON's theories were similar. Their initiator, however, has predicted that by appro-

TABLE 22.

Hypothesis	$F_2$ factorial formula	Frequency in $F_2$ among 16 or 64 offspring	Phenotype in $F_2$	Type of $F_2$ segregation self-col. : mottled : white
KOOIMAN 1	AA BB	1 } 3	self-coloured mottled white	n : — : —
	Aa BB	2 } 3		3 : — : 1
	AA Bb	2 } 6		1 : 2 : 1
	Aa Bb	4 } 6		3 : 6 : 7
	A <sup>a</sup> Bb	3 } 7		— : — : n
	aa B <sup>b</sup>	4 } 7		— : — : n
EMERSON 2	PP <sup>xx</sup> <sub>xx</sub>	2 } 6	self-coloured	n : — : —
	Pp <sup>xx</sup> <sub>xx</sub>	4 } 6	„	3 : — : 1
	PP Xx	2 } 6	mottled	2 : 2 : —
	Pp Xx	4 } 6	„	6 : 6 : 4
	PP <sup>x</sup> <sub>x</sub>	4	white	— : — : n
EMERSON 3	AA PP <sup>xx</sup> <sub>xx</sub>	2	self-coloured	n : — : —
	AA Pp <sup>xx</sup> <sub>xx</sub>	4	„	3 : — : 1
	Aa PP <sup>xx</sup> <sub>xx</sub>	4	„	3 : — : 1
	Aa Pp <sup>xx</sup> <sub>xx</sub>	8	„	9 : — : 7
	AA PP Xx	2	mottled	2 : 2 : —
	AA Pp Xx	4	„	6 : 6 : 4
	Aa PP Xx	4	„	6 : 6 : 4
	Aa Pp Xx	8	„	18 : 18 : 28
	AA pp <sup>x</sup> <sub>x</sub>	4	white	— : — : n
	Aa pp <sup>x</sup> <sub>x</sub>	8	„	— : — : n
	aa p <sup>x</sup> <sub>x</sub>	16	„	— : — : n

priate crosses a decision in favour of any of these two hypotheses might be possible. These crosses should be arranged in such a way that one of the parents is a true-breeding mottled one, the other a race furnishing the factor for ever-segregating mottling, if such a factor exists. If we assume three races I, II and III of which I is true-breeding mottled, whereas II  $\times$  III gives the ever-segregating mottled type, then the crosses I  $\times$  II and I  $\times$  III offer suitable material for a decision.

It will be apparent that in case EMERSON's YZ hypothesis holds good both latter crosses must give a mottled  $F_1$ , segregating into 1 constant mottling  $YZ\ YZ$ , 1 self-coloured  $Yz\ Yz$  or  $yZ\ yZ$  and 2 like  $F_1$ . If however the XM theory holds true we have the following situation.

- Race I  $xxMM$ , Race II  $XXmm$ , Race III  $xxmm$ , or:
- Race I  $XXMM$ , Race II  $XXmm$ , Race III  $xxmm$ .

The crosses I  $\times$  II, I  $\times$  III en II  $\times$  III should give the following results:

TABLE 23.

Case	Cross type	$F_1$	$F_2$	$F_3$ segregations
a	I $\times$ II $MMxx \times mmXX$	mottled or double mottled	2 $MM^{xx}_{XX}$ 2 $MMXx$ mottled or double mottled 4 $MmXx$ mottled or double mottled 4 $Mm^{xx}_{XX}$ mottled 2 $mm^{xx}_{XX}$ self-coloured 2 $mm\ Xx$ mottled	constant mottled 1 constant mottled : 2 double mottled : 1 self-coloured; or constant. segregating like $F_1$ .
	I $\times$ III $MMxx \times mmxx$	mottled	3 mottled : 1 self-coloured	3 mottled : 1 self-coloured. constant.
	II $\times$ III $mmXX \times mmxx$	mottled	2 mottled : 2 self-coloured	2 mottled : 2 self-coloured. constant mottling.
b	I $\times$ II $MMXX \times mmXX$	mottled	3 mottled : 1 self-coloured	constant mottling
	I $\times$ III $MMXX \times mmxx$	mottled or double mottled	exactly like sub case a, cross type I $\times$ II.	
	II $\times$ III, exactly like sub case a, cross type II $\times$ III.			

Cases a and b show exactly the same consequences, widely differing from those of the YZ hypothesis. It is to be regretted that no such

experiments have been carried out. In some crosses, for instance those by SHAW and NORTON in which double mottling is observed, the problem is complicated by the circumstance that red-mottled types have been crossed with yellow-black self-coloured races. This involves so much complications that a decision in favour of either of the mottling theories seems impossible. With respect to the representation of the data considered we may refer to pg. 359 sq., from which the complications involved by the introduction of the factors for red and yellow-black are apparent.

A solution of this interesting problem must be postponed until new data have been obtained.

Here we might still consider the results of MIYAKE a.o. (1930), who adhere to EMERSON's YZ hypothesis. These factors are generally considered to be completely linked. In one of their crosses, however,  $F_1$  of cream and self-coloured was mottled, giving in  $F_2$  mottled, self-coloured and cream offspring in a 2 : 1 : 1 ratio.  $F_3$  generations of several  $F_2$  plants were grown. 61 families from mottled  $F_2$  segregated mottled, self-coloured and cream according to the expected 2 : 1 : 1 ratio; 30 families from self-coloured  $F_2$  bred true; all families from cream bred true. Besides, however, 4 families from mottled gave together 32 mottled and 17 cream offspring; and one family from a self-coloured  $F_2$  gave 7 self-coloured and 4 cream. The authors ascribe these unexpected families to crossing-over. The families, however, are so small that the absence of self-coloured offspring may be considered as a mere chance occurrence. The cream offspring of a self-coloured  $F_2$  plant cannot be accounted for.

#### *True breeding mottling*

We may yet give a few words to this character, without consideration of its possible relation to inconstant mottling. In several crosses it behaves as a simple dominant to solid colours. TSCHERMAK (123, 1912) considers its nature as that of a local suppressor of pigment (eine lokale Hemmung). PLATE (81a, 1915) as that of a distributor of pigment. TJEBBES and KOOIMAN see it as a corrosive factor. Linkage to other factors is not certain, yet from SHAW and NORTON's work we might be inclined to accept a very strong association with the red colour factor. Perhaps also a linkage with one of the brown factors exists, mostly in the form of repulsion.

If we resume the contents of the foregoing pages it seems to reviewer that the most probable solution of these intricate problems is expressed in the following assumptions:

1. True breeding mottling is the effect of a mottling factor  $M$ . This mottling factor acts with most pigments.
2. The mottling factor may be latent in white-seeded races, and besides in buff (= chamois)-seeded ones.
3. Inconstant mottling is caused by the heterogeneous condition of one of the brown chromogenous factors,  $B$ .

If we arrange the data obtained by several experimenters according to the above principles, we get several groups, that are exposed in table 24. Of cause one or the other cross may have been recorded in the wrong group. We have left here out of consideration most crosses in which double mottling has been recorded. With respect to these we may refer to p. 358 sq.

We shall give a few words to the crosses involving Creaseback with the races Blue Pod Butter (cream) and Challenge Black Wax. Blue Pod Butter  $\times$  Challenge Black Wax gives a mottled  $F_1$  of the ever-segregating type. This is equally the case with the crosses with Creaseback. This cannot be explained by the  $YZ$  hypothesis, nor by the  $Bb$  one and points to a different type of mottling. As a matter of fact the mottling in Creaseback crosses is of a special type. SHAW and NORTON (95, 1918) describe it as nearly black, but with faint signs of mottling. In  $F_2$  and further segregations the self-coloured condition seems to dominate, most probably, however many of these self-coloured types are mottled ones, in which the mottling is obscured. This might explain why so much self-coloured plants have mottled ones among their offspring.

TABLE 24.

Cross.	F <sub>1</sub> type	F <sub>2</sub> (D <sub>1</sub> ) or further segregation				Experimenter
		mottled	self-coloured	buff	white	
<i>Group I. Mottled × self-coloured.</i>						
Currie × Golden Wax	mottled	33	9	—	—	EMERSON 22, 1909.
Wardwell × Challenge						
Black Wax . . . . .	id.	29	8	—	—	id.
Red Valentine × Bur- pee stringless . . . . .	id.	160	79	—	—	id.
Burpee stringless × Warwick . . . . .	id.	38	5	—	—	id.
Paris × Non Plus						
Ultra . . . . .	id.	46	18	—	—	id.
Mohawk × Non Plus						
Ultra . . . . .	id.	16	2	—	—	
Mohawk × Scarlet						
Flageolet . . . . .	id.	9	3	—	—	id.
Bunte Ilsenburger × Mont d'or . . . . .	id.	20	6	—	—	TSCHERMAK 123, 1912
Schirmers Cassler × Bunte Ilsenburger .	id.	24	8	—	—	
Rotvioletgeäugte × rotviolette Flageolet	id.	16	4	—	—	id.
Spont. hybr. from Barbès . . . . .	id.	D <sub>1</sub>	8	3	—	KAJANUS 51, 1914.
Several crosses of mott- led and self-coloured varieties . . . . .	id.	ca. 3 :	1	—	—	SHAW and NORTON 95, 1918, table II.
Spont. hybrid of Orange-brown bean	id.	D <sub>1</sub> D <sub>2</sub> D <sub>2</sub> D <sub>2</sub>	52 98 159 300	21 50 60 95	— — — —	TJEBBES & KOOIMAN 113, 1919.
<i>Group II. Mottled × Cream, the latter having M in a latent condition</i>						
Several mottled races						
× Blue Pod Butter	mottled	ca. 3 :	1 (most prob- ably buff)	—	—	SHAW and NORTON 95, 1918, table II.
<i>Group III. Mottled × white, the latter having M in a latent condition.</i>						
Several mottled races						
× Davis, White Mar- row and Navy . . . . .		3	:	1	1	EMERSON 22, 1909.

Cross	F <sub>1</sub> type	F <sub>2</sub> (D <sub>1</sub> ) or further segregation				Experimenter
		mottled	self-coloured	buff	white	

## Group III. Continued.

Violetgeäugte, Marmoriert, × Weisse Ilsenburger . . . . .	mottled	38	—	—	13	TSCHERMAK 123, 1912
Spont. hybr. of Merveille de Vitry . . . . .	id.	52	—	—	12	KAJANUS 51, 1914.
Davis Wax × Keeney Rustless . . . . .	id.	ca. 3	—	—	1	SHAW and NORTON 95, 1918.
Red Valentine × White Marrow . . . . .	id.	ca. 3	—	—	1	id.

## Group IV. Mottled × White, having m (recessive condition).

Jones Stringless × Golden Wax . . . . .	mottled	12	2	—	7	EMERSON 22, 1909.
Chevrier × Bunte Ilsenburger . . . . .	id.	F <sub>3</sub>	22	17	—	id.
Weisse Wachs × Runde violettgeäugte (mottled) . . . . .	id.	7	3	—	2	TSCHERMAK 123, 1912
Several crosses of mottled races with white Marrow and Crease-back . . . . .	id.	39	18	—	27	id.
White × Mottled . . . . .	id.	mottled	self-coloured	—	white	SHAW and NORTON 95, 1918.

## Group V. Crosses between two self-coloured races.

Hundert für Eine × Schwarze Neger . . . . .	mottled	92	75	—	—	TSCHERMAK 123, 1912
„Steninge hybrid“ . . . . .	id.	D <sub>1</sub>	88	108	—	KRISTOFFERSON 60, 1924.
	id.	D <sub>2</sub>	466	475	—	id.
Self-coloured red × self-coloured brown	id.	150	173	—	—	TEN DOORNKAAT-KOOLMAN, 18 1927.

Cross	F <sub>1</sub> type	F <sub>2</sub> (D <sub>1</sub> ) or further segregation				Experimenter
		mottled	self-coloured	buff	white	

*Group VI. selfcoloured × cream, the latter having M in a latent condition.*

Cream × self-coloured	mottled	273	111	121	—	MIYAKE a.o. 75, 1930.
	F <sub>2</sub>	32	—	17	—	id.
	"	616	322	269	—	id.
	"	—	7	4	—	id.

*Group VII. Self-coloured × cream, the latter having m (recessive condition).*

Several self-coloured races × Blue Pod						
Butter . . . . .	mottled	ca. 1	: 1 (including buff)	—	—	SHAW and NORTON 95, 1918.

*Group VIII. Self-coloured × White, the latter having M in a latent condition.*

Davis × Challenge						
Black Wax and recip- rocal . . . . .	mottled	21	6	—	7	EMERSON 22, 1909.
Davis × Non Plus						
Ultra . . . . .	id.	26	15	—	12	id.
White Marrow × Non Plus Ultra . . . . .	id.	25	4	—	15	id.
Non Plus Ultra × Navy	id.	10	9	—	4	id.
Navy × Challenge						
Black Wax . . . . .	id.	7	13	—	8	id.
Non Plus Ultra × Weisse Ilsenburger .	id.	5	2	—	5	TSCHERMAK 123, 1912

*Group IX. Self-coloured × White, the latter having m (recessive condition).*

Non Plus Ultra × White Flageolet . .	mottled	173	164	—	105	SHULL 98, 1908.
Long Yellow Six Weeks × White Flageolet .	id.	193	218	—	160	id.
Prolific Black Wax × White Flageolet . .	id.	59	53	—	44	id.
Spont. hybr. of Métis .	id.	32	30	—	26	KAJANUS 51, 1914.
id.	id.	18	15	—	11	
id.	id.	35	31	—	32	
id.	id.	7	10	—	4	
Chevrier × Non Plus						
Ultra . . . . .	id.	12	10	—	5	TSCHERMAK 123, 1912

Cross	F <sub>1</sub> type	F <sub>2</sub> (D <sub>1</sub> ) or further segregation				Experimenter
		Mottled	self-coloured	buff	white	
<i>Group IX. Continued.</i>						
Mettes Schlachtschwert x Wachsdattel . . .	Mottled	29	13	—	13	TSCHERMAK, 12, 1912.
Chevrier x Schirmers Cassler . . . . .	id.	12	9	—	1	id.
Non Plus Ultra x Wachsschwert . . .	id.	163	167	—	99	id.
Spontaneous hybrid of Flageolet jaune	id.	12	10	—	12	KAJANUS, 51, 1914.
id.	id.	25	36	—	17	id.
spont. hybr. of Mont d'or.	id.	8	12	—	7	id.
Several self-coloured races x Davis Wax and White Marrow.	id.	ca. 9 :	3	:	4	SHAW and NORTON 95, 1918.
Orange-brown x white	id.	F <sub>2</sub>	75	71	58	KOOIMAN 56, 1920
		F <sub>3</sub>	46	26	61	id.
		"	133	70	74	id.
		"	352	364	159	id.
Orange-brown x white	id.		148	131	87	SIRKS 100, 1922.
Orange-brown x white?	id.		15	22	3	id.
Orange-brown x white	id.		82	88	54	id.
id.	id.	F <sub>8</sub>	6	9	5	id.
id.	id.	"	11	14	—	id.
id.	id.	"	18	24	—	id.
id.	id.	"	17	19	—	id.
id.	id.	"	18	21	12	id.
id.	id.	F <sub>2</sub>	76	73	48	id.
Lemon-coloured x white? . . . . .	id.	F <sub>2</sub>	14	9	1	id.
Brown x white . . .	id.		94	101	64	TEN DOORNKAAT- KOOLMAN 18, 1927

*Group X, Crosses between two cream-coloured races.*

Cream x cream . . .	mottled	105	47	118	—	MIYAKE a.o. 75, 1930.
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*Group XI, Cream x white.*

Davis x Blue Pod	mottled	18	4	—	12	EMERSON 22, 1909.
Butter . . . . .	id.	38	19	—	18	MIYAKE a.o. 75, 1930.

*Striping*

This is a type of mottling in which the darker pigment forms a pattern of blots and stripes, the whole giving generally the impression of concentrous striping.

TSCHERMAK (123, 1912) describes a cross of Flageolet Wax, red mottled,  $\times$  Hinrichs Riesen, red striped.  $F_1$  is red mottled,  $F_2$  segregated 4 mottled and 2 striped.

KAJANUS (51, 1914) describes a spontaneous hybrid that is at the same time violet mottled and brown striped. The offspring contains four types: mottled + striped, mottled, striped and self-coloured (very faintly striped and most probably near chamois) in a ratio of about 9 : 3 : 3 : 1. There is apparently no dominance of mottling to striping.

SHAW and NORTON considered light mottling (striping?) as a simple recessive to dark mottling.

TJEBBES and KOOIMAN (113, 1919; 115, 1921) crossed a striped race (Dwarf speckled Cranberry bean) with a self-coloured orange-brown bean. The  $F_1$  was brown-mottled and at the same time striped with purplish red. In  $F_2$ , segregation into three types was observed in a simple 1 : 2 : 1 ratio. The extracted parental types all bred true the  $F_1$  type continued to segregate in the same way. The original solution was that both races might simply differ in factor S (for striping). This, however, involved the assumption of a very complicate action of S: a partial suppression of the brown colour, a partial change of brown into red, when present in a heterozygous condition (Ss), a partial change of brown into red and complete suppression of the rest of the brown pigment in the homozygous condition (SS). This induced the authors to develop a two factor scheme. The yellow bean is represented by Bs, the striped bean by bS. There is absolute linkage between these factors. B in a heterozygous condition causes mottling.

SIRKS (99, 1920) describes the segregation of a spontaneous hybrid of the Dwarf Speckled Cranberry bean (Kievitsboon). This cross, described on pg. 356, is complicated by the great number of colour factors involved and may be here represented in a simplified form. 16 Self-coloured (of which 1 chamois), 37 striped (of which 9 at the same time mottled); 24 white. Striped  $F_2$  individuals were partly

homozygous for striping, partly heterozygous. From his results SIRKS concludes that the striping factor S restricts the purplish red (violet), grey and blue pigment to stripes and that ss beans are self-coloured. In striped beans the background may be chamois, yellow to even bluish brown. When the background is violet or grey it is at the same time mottled. S, according to SIRKS, may be cryptomerically present in chamois, yellow and liver-coloured yellow. This might seem inconsistent with the explanation given by TJEBBES and KOOIMAN. It is however probable that the colours described by SIRKS are not of the same class as those of the yellow bean used by those experimenters (factor B) but belong to the group of C-pigments, that are never mottled on account of the heterozygous (Cc) condition.

TJEBBES and KOOIMAN (115, 1921) observed a spontaneous hybrid between the Pole Cranberry bean and a white seeded race extracted from Hinrichs Riesen. All coloured  $F_2$  and  $F_3$  offspring were striped; besides segregation into 3 striped : 1 white was observed in the expected frequency. It was at that time concluded, that the white bean and the cranberry bean differed in factor S. This explanation is now no longer maintained by the authors. Both types have the factor for striping. The white bean must then be recessive for either the ground-factor for colour (A) or for all chromogenous factors.

#### *The eyed pattern*

All eyed types have in common that only part of the seed coat is coloured by the pigment that forms the eyed pattern. This pigment is always centred about the hilum. In the smallest pattern it may consist of one or a couple of small specks at the caruncle and at the other side of the hilum, in the largest type it may cover nearly the entire seedcoat (in the extreme variants of this type actually so). Nearly all eyed beans show a remarkable degree of symmetry in their pattern. Some of the types are schematically given in fig. 2.

The extension of the eye pattern is characteristic for different races. However within certain limits, as it is considerably influenced by environmental conditions. PEARL and SURFACE (81, 1915) studied the variability of the eye character in yellow eye beans and tried to establish standard types (see fig. 2, 7 and 8). OWEN a.o. (80, 1928) however found that rich soil and wide spacing of the plants in-

creased the extension considerably in the races investigated (Small Yellow Eye and Old-fashioned Yellow Eye). In one other race (Golden

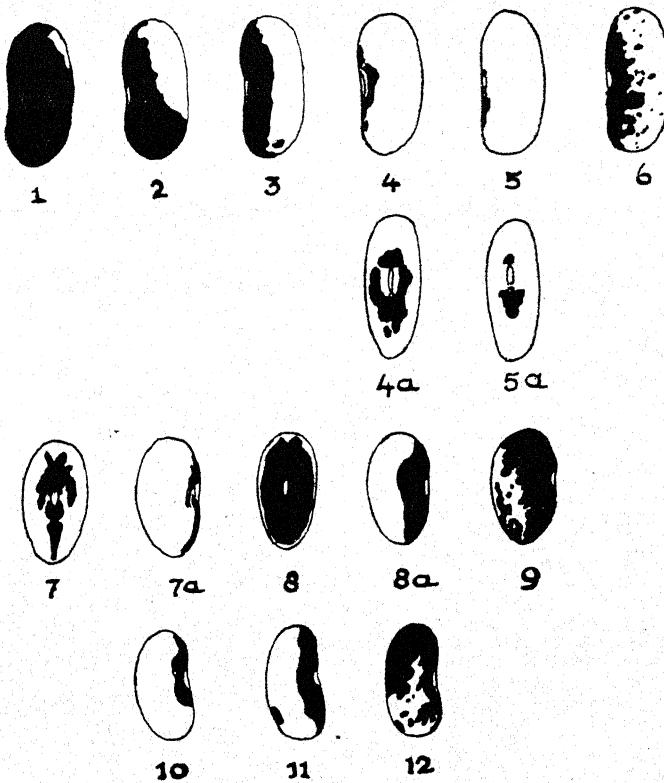


FIG. 2. Types of eyed patterns.

1—6 after MIYAKE. 1—2, bald; 3 saddle; 4—5 (small) eye; 6 speckled; 7—8 after PEARL and SURFACE. 7, standard type of Old-fashioned Yellow Eye; 8 standard type of Improved Yellow Eye; 9, heterozygous type between 7 and 8. 10—12 after TSCHERMAK. 10, formula  $z_1z_1z_2z_2$ ; 11, formula  $z_1z_1Z_2Z_2$ ; 12, formula  $z_1z_1Z_2z_2$ .

Wax) this influence was much less, whereas Golden Carmine was not perceptibly influenced.

Other pattern types may be combined with the eyed one. Thus striped, mottled and solid eyes may be distinguished. The ground colour is usually white; yet self-coloured backgrounds (perhaps only ecru) are observed.

The first report on the inheritance of the eye character is by EMERSON (22, 1909). In four different crosses of eyed with totally pigmented races he observed complete dominance of the totally pigmented condition, segregation in  $F_2$  and following generations into totally pigmented and eyed types, more or less conform the 3 : 1 ratio ( $F_2$  64 : 30;  $F_3$  72 : 25). In crosses of white with eyed beans he obtained in all of his crosses totally pigmented  $F_1$  offspring. This proves that all white seeded races used by him (Navy, Davis and Jones Stringless) are homozygous for the extension factor (T) that distinguishes totally pigmented from eyed types. In  $F_2$  segregation into totally pigmented, eyed and white beans occurred. It may be expected that the whites are different with respect to this extension factor (TT, Tt, tt). Back crosses between extracted whites from the cross Navy (white)  $\times$  Wardwell (eyed) with homozygous eyed races proved the existence of these different types. The back cross generations gave either merely self-coloured, self-coloured and eyed or merely eyed offspring. (EMERSON 23, 1911).

TSCHERMAK (123, 1912) published his results of some crosses with the eyed race "Runde geäugte".  $F_1$  in all cases was totally pigmented. Weisse Wachs  $\times$  "Runde geäugte".  $F_2$ : 47 total pigm., 10 eyed, 27 white. Runde geäugte  $\times$  rotviolette Flageolet.  $F_2$ : 19 total pigm., 1 eyed.  $F_3$  (4 small segregating families taken together) 85 tot. pigm., 16 eyed.  $F_4$  (4 small families together) 37 tot. pigm., 10 eyed. Runde geäugte  $\times$  Weisse Ilsenburger.  $F_2$ : 26 tot. pigm., 12 eyed, 13 white. In the crosses 1 and 3 the segregation is apparently (as far as the eye character is concerned) monohybrid, in the second cross this is doubtful.

TSCHERMAK distinguished four classes among his eyed types. 1.  $\frac{1}{4}$  to trace of white; 2.  $\frac{1}{4}$ — $\frac{1}{2}$  white; 3.  $\frac{1}{2}$ — $\frac{3}{4}$  white;  $\frac{3}{4}$ —nearly totally white, and he proposes two extension factors  $Z_1$  and  $Z_2$  to explain his observations. The factorial compositions of his three main types is then as follows:

$z_1 z_1 z_2 z_2$  restriction of pigmentation to small eye about the hilum  
 $z_1 z_1 Z_2 Z_2$  about  $\frac{1}{2}$  white  
 $z_1 z_1 Z_2 z_2$  about  $\frac{1}{4}$  white.

All  $Z_1$  forms are totally pigmented. Consequently this factor is identical with EMERSON'S T.

In this hypothesis it is most remarkable, that the  $\frac{1}{4}$  white type is

the heterozygous form between small eye and medium eye (fig. 2, 10—12). This has been corroborated by an observation by SURFACE (105, 1916) of spontaneous hybrids between the medium eyed race Improved Yellow Eye and the small eyed Old-fashioned Eye. The hybrid seeds of first generation plants were always large-eyed of a peculiar spotted type called "piebald" (fig. 2, 7—9). These piebalds segregated in the second generation into the parental types and piebald. In all cases the parental types bred true and piebalds segregated. In all cases, however, there was a deficiency of Improved yellow eye types, which fact is explained by the assumption of a lethal factor L. This L is lethal for the Improved Yellow Eye when present in a double dose (LL), but does not affect the viability of the other types. The observations of TSCHERMAK have also been corroborated by SAX and MCPHEE (91, 1923) who do not mention a deficiency of Improved Yellow Eye, but consider the segregation apparently as a regular 1 : 2 : 1 one, without giving actual data.

KAJANUS (51, 1914) observed the following segregation from a totally pigmented spontaneous hybrid of the eyed race Métis:

32 totally pigmented : 8  $\frac{1}{2}$ -nearly totally pigmented : 2 small eye. His suggestion of 3 extension factors is not sufficiently founded. TSCHERMAK's assumption might well cover the facts.

SHAW and NORTON (95, 1918) also considered the inheritance of the eyed condition. In crosses of totally pigmented and eyed beans dominance of the former and simple 3 : 1 segregation in further generations is probable, though an excess of totally pigmented beans is found. In all crosses of eyed with white beans  $F_1$  has been totally pigmented,  $F_2$  has segregated into totally pigmented, eyed and white beans.

The authors assume two factors; P the pigmentation factor, T, a factor that extends the factor over the entire seedcoat. Thus PT is entirely pigmented, Pt is eyed, all p forms are white. They further state that at least four racial types of eyes exist: very small eye Ptrs, small eye PtRs, medium eye PtrS, large eye PtRS; they do not distinguish these types in the presentation of their data or present any other foundation for this RS hypothesis.

SAX (87, 1923) made some crosses between eyed and white beans that need special attention. The results are represented in table 25.

TABLE 25.  $F_2$ 

Type of Cross	$F_1$	totally pigm.	eyed	white
Improved Yellow Eye 1310 $\times$ White 1333 . . . . .	totally pigmented	201	68	80
theoretically . . . . .		9	3	4
Dot Eye 1902 $\times$ White 1228 .	id.	194	28	67
theoretically . . . . .		45	3	16
Improved Yellow Eye 1317 $\times$ White 1228 . . . . .	id.	126	12	41
theoretically . . . . .		45	3	16

The theoretical proportions, suggested by the author indicate the assumption that the eyed condition might be either a simple or a double recessive to total pigmentation. The actual data though not beautifully agreeing with the latter assumption at least strongly indicate factorial relations that are more complicate than a one factor difference between the races involved.

In a second paper (91, SAX and MCPHEE, 1923) a cross between very small eye and white is demonstrated.  $F_1$  was totally pigmented (mottled) and gave rise to an extremely varied  $F_2$  generation that contained totally pigmented and white types besides a large series of different eye sizes. Actual data are not presented.

MIYAKE a.o. (75, 1930) distinguish among eyed (or wrongly denominated by them "Piebald") races the following types: 1. bald = more than  $\frac{1}{2}$  of the seed coat coloured; 2. saddle = less than one half of the seedcoat coloured; 3. eye = small eye of other investigators. "Piebald" behaves as a simple recessive to totally pigmented. Saddle  $\times$  bald gave bald  $F_1$ .  $F_2$  segregated into 12 bald : 3 saddle : 1 eye. In a cross of the same bald strain with a mottled race the  $F_2$  segregation seems to be conform 9 : 3 : 4. In the same paper a "speckled" type is described in which small dots of pigment cover the white area of the "piebald" seed. In a cross of "speckled piebald"  $\times$  "piebald" the former type is fully dominant, giving in  $F_2$  a clear cut 3 : 1 segregation. Whether "speckling" ever occurs apart from the "piebald" type is not stated. Perhaps it might be considered as a modifier of any eyed condition.

The eyed conditions seems to be related to a number of other characters. In all crosses cited above, white types proved to carry a factor for total pigmentation. This might point to a relation between one of the pigmentation factors and T. As EMERSON's back cross experiment has shown that this is not the case it must be explained by a less general distribution of the eye character among commercial bean varieties. From the chapter on flower colour a relation between eye and flower colour is apparent (see p. 316). It equally may be related to vine type. In the third place it seems to be related to one of the size factors (see p. 392 sq.).

If we reconsider the facts cited above we may conclude that a factorial scheme that is generally applicable cannot with any degree of reliability be furnished.

#### *Obscuratum Phenomenon*

This phenomenon, named *obscuratum* at the suggestion of KAJANUS, is to my knowledge first mentioned by HOFFMANN (39, 1874) in the bush bean varieties: *Phaseolus vulgaris sphaericus haematoecarpus* (seed coat purplish ecru with purple stripes), "Zebrabohne", ecru-coloured with black stripes and (40, 1879) Passeyr-Bohne and other striped races. The phenomenon consists in the extension of the darkest coloured parts, to such a degree that the seed-coat appears nearly self-coloured. HOFFMANN did not succeed in fixing this character. KAJANUS (1914) observed the same phenomenon in several mottled varieties and studied the offspring of normally mottled and *obscuratum* seeds. He concludes that most probably developmental factors cause the phenomenon. The character is not hereditary.

SHAW and NORTON (95, 1918 p. 98) give the following statement that, though in my opinion too careless for such an interesting problem and only of doubtful value, should not be passed unnoticed. "Among these light mottled progeny [of Blue Pod Butter  $\times$  Davis Wax] there appear some plants that produce what seem to be bud sports, in which the darker reddish color predominates over the surface of the bean. They may appear as single pods or as branches bearing several pods, and rarely a portion only of the beans in a single pod is affected. If these dark mottled beans are planted they breed true to seed coat color, while the plants with light mottled seed

may breed true in this character, or may give rise to plants bearing bud sports as before. Limited observations suggest that these sport-ing plants exist in definite proportions".

TJEBBES (108, 1921, 110, 1923) gives a report on the same question in a striped variety, the Dwarf Speckled Cranberry Bean (Kievits-boon). He observed sectorial distribution of normal and obscuratum beans.

The author is of the opinion that we have to do with a sectorial chimaera, restricted to the epidermis from which the seed coat originates. To this restriction the non-hereditary character of the obscuratum phenomenon is ascribed.

The phenomenon however is not restricted to *Ph. vulgaris* races. TJEBBES (111, 1925) found it also in plants with striped seeds of the species *Ph. multiflorus*. Here again the distribution is sectorial, the character non-hereditary.

#### *Seed coat colour in Phaseolus multiflorus*

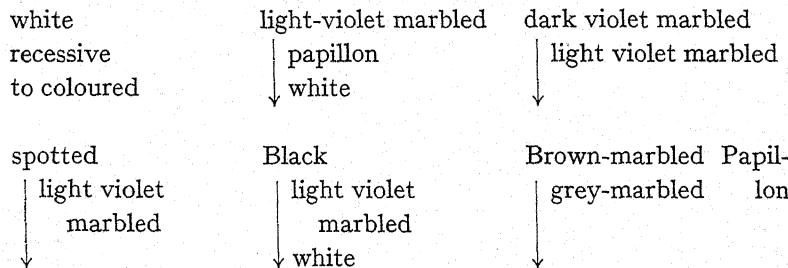
It is generally recognised that white, here too, is recessive to the coloured condition. This may already be concluded from the earlier observations by FERMOND (26, 1855), as well as from those by LENZ (63, 1920) on spontaneous hybrids. As, however, unprotected plants will again be inclined to be cross-fertilised, white-seeded offspring will tend to produce a smaller or larger percentage of coloured-seeded plants. This doubtless is the cause of REINKE's (83, 1915) erroneous statement of the dominance of the white seed-coat character. TSCHER-MAK (122, 1904, p. 584) reports on a cross of a race with blackmarbled seeds on a red ground colour with a white-seeded race and reciprocal.  $F_1$  in both cases was as the coloured parent,  $F_2$  gave both types in a 3 : 1 relation. The same coloured races fully dominated in  $F_1$  over the brown marbling of papillon seeds.

SIRKS (100, 1922) did not succeed in crossing a white-seeded white-flowering variety with red-flowered ones; moreover he states that spontaneous hybrids in the white variety did not occur, though both types were grown side by side during four years. From seed obtained from the trade he was able to isolate six different types:

1. Flowers, red, seeds black marbled upon light-violet ground.
2. " " " " " " dark-violet ground.

3. Flowers red, seeds with small black spots upon light-violet ground.
4. " " seeds black.
5. Flowers red (banner) and white (wings), seeds brown-marbled upon yellow-white ground (Papillon).
6. Flowers red and white, seeds grey-marbled upon yellowish-white ground.

Most of the plants of these several types bred true, some segregated. As the plants have not been protected against cross-fertilisation, hybrids must have occurred on a comparatively large scale. SIRKS indicates as probable hybrids not less than 72 among 968 descendants from coloured-seeded motherplants. Yet he provisionally indicates some dominance-relations.



The work of TJEBBES (111, 1925) is by far the most interesting publication on this species. He reports on two crosses.

1. White-seeded, long-podded  $\times$  Red flowering, black-mottled (Weisse Langschötige)

purple seeds.

13  $F_1$ -plants were intercrossed and produced seeds that were nearly like those of the pollen race, yet differed from them in that the marbling was only intensively black near the hilum whereas it was greyish black at the periphery. TJEBBES calls this "abgestuft". I will indicate this type as "shaded".

The results together with the theoretical interpretation are given in table 26. This interpretation is based on the following hypothesis. a, Au and Ad form a series of multiple allelomorphs of which both Au and Ad, when in a homozygous condition strongly diminish the viability. The different types of seed-coat colouring are suggested to be:

White aa

Shaded Au a, Ad a, Au Au

Dark Ad Ad, Au Ad.

TABLE 26

Bibliographia Genetica VIII

Now TJEBBES supposed that the result of intercrossing 13  $F_1$  plants ( $\underline{A}u\ a + \underline{Ad}\ a$ ) is the same as that of the cross  $\underline{A}u\ a \times \underline{Ad}\ a$ . This is not quite true. In reality the offspring consist of those of the following three crosses  $\underline{A}u\ a \times \underline{A}u\ a$ ,  $\underline{A}u\ a \times \underline{Au}\ d$ ,  $\underline{Au}\ d \times \underline{Au}\ d$ . Supposing that 6  $\underline{A}u\ a$  and 7  $\underline{Ad}\ a$  individuals have been intercrossed at random, than the results would be 13 white : 26 shaded : 7 dark or (if  $\underline{A}u\ \underline{A}u$  and  $\underline{Ad}\ \underline{Ad}$  are excluded) 3 white : 6 shaded : 1 dark. Of course very large deviations from this scheme are allowed and the results obtained by TJEBBES fall easily within its limits.

It might here be of importance to point to the theoretical interest of this case with respect to observed cases of self-sterility and self-fertility (p. 299) and the production of different classes of  $F_1$  hybrids in the case of the cross *Ph. vulgaris*  $\times$  *multiflorus* (p. 00).

2. Red-flowering, black mottled seeds  $\times$  white-flowering, white-seeded variety from Chile.

$F_1$ , seeds shaded and striped at the same time.  $F_2$  segregated into:

white:	$\underline{aa}\ \underline{S}\ \underline{b}$
shaded:	$\underline{Au}\ a\ \underline{S}\ \underline{S}\ \underline{b}$ ; $\underline{Au}\ a\ \underline{s}\ \underline{b}$ ; $\underline{Ad}\ a\ \underline{s}\ \underline{b}$ .
shaded and striped:	$\underline{Ad}\ a\ \underline{S}\ \underline{s}\ \underline{b}$
dark mottled:	$\underline{Au}\ \underline{Ad}\ \underline{s}\ \underline{b}$
dark mottled and striped:	$\underline{Au}\ \underline{Ad}\ \underline{S}\ \underline{s}\ \underline{b}$
striped:	$\underline{Ad}\ a\ \underline{S}\ \underline{S}$ ; $\underline{Au}\ \underline{Ad}\ \underline{S}\ \underline{S}\ \underline{b}$

nearly self black: all ss-forms that have B.

The factors a,  $\underline{Au}$  and  $\underline{Ad}$  are known from the previous cross. The action of factors S and B may be inferred from the formulas ascribed to the several types. As the data are not numerous the explanation is not to be seen as conclusive, but only provides us with a useful working hypothesis.

*Seed-coat colour in the hybrids of Phaseolus vulgaris and multiflorus.*

Spontaneous hybrids have repeatedly been reported (see p. 321); in all these cases *Ph. vulgaris* apparently has entered the cross as a ♀. As a matter of fact artificial hybridisation between both species is easy with *vulgaris* as the female parent, whereas the reciprocal cross is more difficult to perform. TEN DOORNKAAT-KOOLMAN (18, 1927)

reports that the cross with *vulgaris* as a seed parent was successful in 25 % of pollinations, the reciprocal cross however only in 5 out of 62 pollinations, or 8 %.

MENDEL (74, 1865) crossed *Ph. nanus* (= bush bean) ♀ with white flowers and white seed coat × *Ph. multiflorus*, scarlet runner bean. The  $F_1$  was nearly like *multiflorus*, the flowers, however, were less bright. According to limited fertility the second generation was small. *Vulgaris*-characters reappeared; the material could however not be analysed as the segregation was too complicated with respect to the few offspring. Length of axis and form of pod showed simple 3 : 1 segregation. Of seed-coat colours MENDEL mentions white, mottled as in *multiflorus*, self brown, dark brown, black brown and black.

KÖRNICKE (58, 1876), observed a spontaneous hybrid *Ph. vulgaris* ♀ × *multiflorus*, that was almost identical with the pollen parent. The offspring of this hybrid all resembled *vulgaris*, from which fact KÖRNICKE concluded that the plant had been fertilised by *vulgaris*.

TSCHERMAK obtained several artificial hybrids, one of which with *Ph. multiflorus* as a seed parent. In his first cross of the bush bean Wachsdattel ♀ × *Ph. multiflores* ♂ the  $F_1$  was much like *multiflorus* (description 120, 1901, p. 717—718). Other crosses are described in a further publication (122, 1904, p. 622). In the same paper extensive  $F_2$ — $F_4$  data are to be found. The results have been summarized by the author in a still later publication (123, 1912). Here the author remarks: "Es muss jedoch bezüglich der ganzen bisher gewonnener Daten der Bastardierung *Ph. multiflorus* × *Ph. vulgaris* zugegeben werden, dass die Wahrscheinlichkeit einer Verunreinigung durch nachträgliche ungewollte Fremdbestäubung eine sehr grosse ist ....". In view of the doubtless frequent cross-pollinations of a large part of the offspring the data are untrustworthy, and the reviewer may safely omit their representation.

TJEBBES (112, 1927) publishes the results of three crosses:

1. Yellow brown bush bean (one of JOHANNSEN's lines) × Scarlet runner bean.
2. Chevrier, bush bean with greenish seeds × white seeded *multiflorus*.
3. Chevrier × Scarlet runner bean.

Considerable sterility here again prevented satisfactory analysis. In cross 1  $F_1$  plants produced seeds like those of the *multiflorus*

parent, the ground colour, however, was very dark purplish red. The  $F_2$ -generation consisted of 8 plants, the seeds of which were

2 black mottled upon greyish yellow ground

2 white

4 like  $F_1$ .

In  $F_3$  the  $F_2$ -plants of  $F_1$  type gave white, different brown self colours, black self, and mottled types, more or less like Scarlet runner. From these results TJEBBES concludes that most probably the parent types have different ground-factors for pigmentation, which might explain the relative frequency of white-seeded  $F_2$ -offspring<sup>1)</sup>. Further he suggests that they have no colour factors in common and that the different colours of  $F_2$  and  $F_3$  are due to addition of both colour-series.

Cross 2 only produced  $F_1$  plants with a few seeds that did not produce mature plants. The seeds were reddish grey turning into dark red-brown. TJEBBES concludes to the presence of an intensifying factor I in Chevrier.

Cross 3 gave  $F_1$ -plants with seeds of multiflorus type with darker ground.  $F_2$  consisted of 17 mottled more or less like *multiflorus*, 4 self black, 3 reddish grey-brown, 9 white. For this cross the author presents as a working-hypothesis the following factorial explanation:

White:	$PP^a I^i$
black:	$P^p P^a II$
brown:	$P^p aa I^i$
mottled:	all other formulas.

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<sup>1)</sup> TSCHERMAK (123, 1912) and HALSTED (36, 1906; 37, 1907 cited after EMERSON) also observed the segregation of whites, but as in both cases this was first observed in  $F_4$ , we may safely suppose spontaneous crossing of  $F_2$  plants with the white-seeded race.

## CHAPTER VII

### QUANTITATIVE CHARACTERS

#### *Seed weight and form; dimensions*

As such we may consider seed weight, absolute length, breadth and width, and relative length, breadth and width. All such characters are to a considerable degree subject to variation, especially so the absolute measures and weight. As to the conditions that influence these quantitative characters we may simply point to wheather conditions (TAVČAR, 106), soil conditions, internal conditions. Thus HARRIS (38b, 1915) has shown that the seed weight is correlated with the relative position in the pod, as well as with the number of seeds per pod.

This implies that the genetical investigation of these characters requires all sorts of precautions in order to yield comparable values: on the one hand data to be compared should be taken from material grown in the same year, under as nearly as possible identical conditions; on the other hand an elaborate laboratory technique of weighing and measuring, and a mathematical technique of computation had to be developed in order to characterize the material by some few figures.

These problems cannot be considered here. We must restrict ourselves to the brief representation of some facts and theories that either historically or from the standpoint of the experimenter interested in the genetics of beans are of interest.

Soon after the rediscovery of Mendel's laws JOHANNSEN started his famous experiments concerning the heredity of quantitative characters in beans. At that time Galton's law of filial regression had lost its explanatory power with respect to qualitative characters, but was still arduously defended by biometricalists and zoologists with respect to quantitative characters.

JOHANNSEN (45, 1903) carried out his experiments in the first place in order to decide whether GALTON's law of regression holds true for such characters. His method was that of a biological analysis of a population of selffertilizing plants. As such he considered, though not quite correctly, *Phaseolus vulgaris* (Cf. pg. 300 especially LENZ 63, 64 and SCHIEMANN 93). For such a population, as for any other population, GALTON's law holds good; selection within such a population is able to shift the type in the direction of the selection. Selection, however, will immediately result in the separation of "pure lines" if only the offspring of any individual is harvested separately; within such a "pure line" selection has no effect at all. In other words selection of a fluctuation is not able to shift the type. Thus JOHANNSEN proved that GALTON's law is not a biological but merely a statistical law.

On account of the foregoing the question was raised whether intercrossing of pure lines augments the range of fluctuation "in respect of such quantitatively estimated characters which (at least in the first generation of hybrids) blend in hybridisation". JOHANNSEN (46, 1906) tried to solve this point by intercrossing some pure lines of beans and by comparing the weights and measures of the seeds of the pure lines with those of the hybrid offspring (SG II)<sup>1)</sup>.

Here, however, we have to face a problem which, apparently overlooked by JOHANNSEN, in 1922 was seriously considered by TSCHER-MAK (129). In a homozygous selffertilizing plant the embryo, contained in selfed seeds, has the same genotype as the mother; if hybridisation takes place there is a difference in genotype between them. The weight of such a seed may in the first place be determined by the mother plant, on the other hand the possibility may be supposed that it is influenced by the properties of the embryo. Though, however, JOHANNSEN expressly states that "a germ produced by intercrossing is developed in a testa belonging to the mother plant" he seems to have taken for granted that the physiological and genotypical properties of the seed parent are the sole determiners of the quantitative properties of the seed. As a matter of fact the comparison of the weights and measures of the pure lines with those of seeds harvested from  $F_1$ -plants (containing  $F_2$  embryos) seems to prove that there is no increase of fluctuating variability offering any better material for

<sup>1)</sup> SG means seed-generation. Thus SG<sub>I</sub> are the hybrid seeds produced on the mother plant of the original cross. SG<sub>II</sub> the seeds born by  $F_1$ -plants etc.

selection. From his three crosses I cite the data considering seed weight.

	n	A (verage) (centigrammes)	$\sigma$	Coefficient of variability (V)
Pure line SE . . . . .	414	36.9	6.47	17.5
SE $\times$ E (S.G.II) . . .	902	46.6	7.34	15.7
Pure line E . . . . .	446	59.7	6.25	10.5

From these data it may be safely concluded that the hybrid mother plant causes no material increase of variability among the seeds it produces; further that the mother plant determines the seed-weight to such a degree that the genotypical differences with respect to seed weight determiners contained in the embryo's are nearly or absolutely suppressed.

It is interesting to compare JOHANNSEN's results to those obtained by TSCHERMAK (129, 1922) with his cross

#### Zucker-Reisperl $\times$ Anker

	n	A	$\sigma$	V
Zucker Reisperl ♀ . . . . .	1193	10.026	$\pm$ 2.3502	23.4
Anker ♂ . . . . .	257	57.32	$\pm$ 7.051	12.3
SGI . . . . .	30	19.61	$\pm$ 2.46	12.5
SGII (6 plants) . . . . .	931	25.96	$\pm$ 7.0855	27.3
SGII separate plant . . . . .	96	24.377	$\pm$ 7.597	31.2
SGII " " . . . . .	155	27.85	$\pm$ 7.029	25.2

Here matters are considerably complicated by the great difference in seed weight between both parents, most probably mainly determined by one single pair of allelomorphs (or closely linked groups of allelomorphs).

From these data TSCHERMAK<sup>1)</sup> concludes that the seeds of the first seed generation (SGI), though intermediate between those of

<sup>1)</sup> See also TSCHERMAK's publications on *xenia* (126, 1919 and 131, 1931).

the parent races, show a certain degree of metrokliny. The fluctuating variability has not increased in comparison to that of Zucker-Reisperl. In SGII TSCHERMAK observes segregation with respect to seed weight: even within the same pod small, intermediate and large seeds are found side by side. It is however to be regretted that on account of a highly unsatisfactory way of graphical representation the probable bimodality of distribution is not demonstrated. The coefficient of variability is considerably increased, even surpassing the value of the father race. In SGIII the segregation becomes clearly evident, the average and standard deviation ranging from  $48.7 \pm 8.708$  to  $9.79 \pm 1.99$ .

In a reciprocal cross of Zuckerperl—Perfection and Flageolet Victoria, of which no data are given, TSCHERMAK did not observe these phenomena. He concludes provisionally that in this case the seed weight is apparently solely determined by the seed bearer. Consequently the latter case may be comparable to that of JOHANNSEN.

As we have seen TSCHERMAK observed in one of his crosses a rather marked metrokliny. SIRKS (102, 1925) expresses as his opinion that the decrease of the seed weight is the result of an inhibiting factor present in the small seeded white race. From unpublished results SIRKS concludes "that these SGI-seeds will be a little heavier than the selfed seeds if the motherplant is a light- and white-seeded one, but that they will show a rather strong metrokliny; if the pollen-parent is of a light- and white-seeded race, while the motherplant is a coloured and heavy-seeded one, then the SGI-seeds will be more or less intermediate".

SAX (87, 1923), studied the inheritance of seed weight in relation to pigmentation factors of the seed coat in  $F_2$ - and  $F_3$ -generations. He crossed small white-seeded with large eyed beans and observed segregation into four classes: mottled, self-coloured, eyed and white. His results are given in the following table.

I	Parents			
	♀	Weight	♂	Weight
Improved Yellow Eye 1310		$56 \pm .5$	White 1333	$28 \pm .9$

$F_2$  segregates

Mottled	Self	Eyed	White
$39.1 \pm .4$	$36.5 \pm .5$	$39.0 \pm .4$	$33.8 \pm .4$

## II

## Parents

♀	Weight	♂	Weight
Dot Eye 1902	$58 \pm 1.2$	White 1228	$21 \pm .2$

 $F_2$  segregates

Mottled	Self	Eyed	White
$27.8 \pm .4$	$27.7 \pm .4$	$26.6 \pm .5$	$23.4 \pm .5$

## III

## Parents

♀	Weight	♂	weight
Improved Yellow Eye 1317.	$48 \pm .5$	White 1228	$21 \pm .2$

	Mottled	Self	Eyed	White	Coloured Homo- zygous	heter- zygous
$F_2$ segregates	$28.8 \pm .4$	$28.6 \pm .6$	$31.3 \pm 1.1$	$26.4 \pm .5$	$30.7 \pm .6$	$28.3 \pm .3$
$F_3$ segregates	$29.2 \pm .1$	$29.0 \pm .1$	$30.2 \pm .2$	$25.8 \pm .1$		

From these data SAX concludes that a size factor is associated with the pigmentation factor P and that this factor in double dose has approximately double the effect of one factor, indicating no dominance of size factors. He further suggests that in Improved Yellow Eye a size factor is associated with the extension (eye) factor T, as the eyed offspring have an increased weight above self coloured

beans. Possibly in cross I a third size factor is, according to SAX, who adheres to SPILLMAN and EMERSON's hypothesis, associated with both mottling factors Y and Z, introduced by the white seeded parent.

Of these conclusions the association of a size factor with the pigmentation factor P was corroborated by SIRKS (102, 1925) in a technically superior treatment of data. Of 59  $F_2$  plants all seeds were weighed.

	Extremes	Mean of all Means	n
White . . . . .	$31.68 \pm 0.74$ — $48.39 \pm 0.63$	38.20	21
Heterozygous coloured	$31.76 \pm 0.45$ — $47.78 \pm 0.62$	40.35	24
Homozygous coloured.	$38.17 \pm 0.62$ — $53.16 \pm 0.98$	43.76	14

From the graphical representation of the differences between the means of all the coloured and of all the white seeded plants in mixed  $F_3$  generations we see at a glance that in most cases the coloured seeds have a larger seed weight. Only in a few families the weight of the white seeds surpasses that of the coloured ones. The facts strongly point to a linkage relation with a certain amount of crossing-over. The existence of crossing-over was equally evident from the occurrence of exceptional heavy whites in families with prevalently small-seeded whites. SIRKS further tries to show that this size factor I should be considered as an inhibitor linked to the pigmentation factor. In my opinion this is immaterial as automatically the allelomorph *i* might then be considered as a growth stimulating factor.

The seedweight has of course to be considered as a function of the absolute dimensions. The inheritance of these dimensions has been studied by JOHANNSEN with respect to the same problems as have been considered in the pages devoted to seed weight. We consequently need not review these data.

MALINOWSKI (68, 1921), in a paper written in Polish, with the contents of which I could acquaint myself only from the french summary, considers the inheritance of seed dimensions in a number of crosses between 20 varieties. The data obtained permitted their arrangement into three groups that are, however, not very sharply distinguished.

1.  $F_1$  plants produce seeds that are intermediate between those of

the parent plants. The  $F_2$  segregation is intermediary, that is, the segregated types remain well within the limits of the parent races.

2. Transgressive segregation. Several types are segregated in  $F_2$ , part of which transgress the limits of variation of the parent type with smallest dimensions, part of which transgress the limits of the parent type with largest dimensions.

3. Asymmetric transgressive segregation, considered as a special case of heterosis (see pg. 306). This case is represented by the crosses Hinrich's Riesen  $\times$  Bagnolet and by Flageolet rouge  $\times$  Bagnolet. In both cases the  $F_1$  plants had seeds equal to the largest seeded parent Bagnolet. In  $F_2$  transgressive segregation occurred as in case E<sub>2</sub>, with only this difference that types transgressing the limits of Bagnolet, were much more frequent than those transgressing the limits of the parent with small seeds. Just the reverse was observed in the case of a cross between Krolowa  $\times$  Japonska.

The seed form may be considered as a function of relative dimensions. TSCHERMAK (124, 1916) simply states the prevalence of the cylindrous seed form over round and kidney shape, and in every case "impure segregation".

MALINOWSKI stated that there is apparently a strong (absolute?) degree of linkage between the factors which determine the seed dimensions. This explains, according to MALINOWSKI why all types might be included in such a simple scheme as that of COMES:

1. *Phaseolus vulgaris* L. var. *compressus* (DC) COMES
2. " " " *ellipticus* (MARTENS) COMES
3. " " " *oblongus* (SAVI) COMES
4. " " " *sphaericus* (SAVI) COMES.

He suggests the following hypothesis, that to some extent may serve to illustrate his point of view:

For a certain seed type, say *compressus*, the factors may be

A, B, C .... for length

P, R, S .... for breadth

X, Y, Z .... for width.

The factors A, P and X; B, R, and Y; C, S and Z, etc. are supposed to be strongly or even absolutely linked.

It is doubtful whether this hypothesis is valuable. The results of TAVČAR (107, 1926) at least do not agree with it. This author states that the seed dimensions of the parental types reappear in the off-

spring in different combinations; the coefficients of correlation, however, point to a certain degree of linkage between the factors determining seed dimensions. Perhaps also MALINOWSKI seems to have observed some facts that point to only relativ coupling. Such is suggested by his statement: "Je suppose l'existance de 3 facteurs cumulatifs produisant la forme courbée en rognon chez les Semences de la variété "Rognon de Coq"."

As to the number of size factors involved in several cases. TSCHERMAK estimates them to be at least 2, more probably 3. SAX estimates the number by several methods, which give 4—6 and even more. However he considers these results as of little or no value. SIRKS shows us a way in which an estimation might be possible. He determines the number of genotypical groups within any family. Two plants may be judged to belong to different genotypical groups if the difference between their mean values is greater than  $3\sqrt{mE_1^2 + mE_2^2}$ . This method gave for his  $F_3$  families numbers of genotypical groups ranging from 3 to 14. Of course these are least values. From these least values it might be possible to calculate a least value of the number of factors involved.

### Xenia

In his case of the cross Zucker-Reisperl  $\times$  Anker TSCHERMAK designates the SG1 seeds rightly as xenia. The first author who reports to have observed xenia in bean crosses (J. DANIEL, 11, 1912) doubtlessly misinterpreted his material. This author fertilized *Phaseolus multiflorus* (seeds mottled violet and yellowish white) with a black-seeded bush bean. The SG1 consisted of two black seeds (considered to be xenia), producing two plants exactly equal to *multiflorus* and considered to be unilateral hybrids. The offspring of the plants grown from these two seeds germinated all of them with hypogeous seed-lobes. Of the seedlings 96 were pale green, 267 tinged with violet-brown. Most probably the original seed parent has been a hybrid with a black-seeded *multiflorus* and the cross with *Ph. vulgaris* has failed. TSCHERMAK's observation has been corroborated by TAVČAR (107, 1926) who observed seed xenia in a cross of the pure lines of "Pabstfisolen" and "Weisse Ilsenburger".

*Earliness and productivity*

In a paper of principally practical value ZWEEDE (138, 1929) shows that considerable differences in earliness and productivity exist within a line of beans, that had been selected 14 years before by SPRENGER. These differences are of a hereditary nature.

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## CHAPTER VIII

### IMMUNITY AGAINST DISEASES

As this subject should rather be treated in a general monograph on the heredity of immunity I may be allowed to give a general statement of the problem without attempting a complete review of the extensive literature. A rather complete list up to 1927 is given by TEN DOORNAAT KOOLMAN (1927). Further I may in a general way refer to papers by BARRUS (1, 1911; 2, 1918) and SCHAFFNIT (92, 1925). The degree of susceptibility of beans to infection by *Colletotrichum Lindemuthianum* depends at least on three conditions: external conditions under which the beans are grown, the racial character of the beans and the special strain of the fungus. Only the latter two conditions will be considered here.

Of *Colletotrichum Lindemuthianum* different strains exist. BARRUS (2, 1918) isolated two strains ( $\alpha$  and  $\beta$ ), McROSTIE (67, 1919) a third strain ( $\gamma$ ). TEN DOORNAAT KOOLMAN used in his experiments 10 strains of European origin of which 9 perhaps were identical. At any rate the actual number of physiologically different strains may be considerably greater than those tested.

These strains may be distinguished in that different bean races behave differently when infected. This is nicely illustrated by LEACH (62, 1923) in the following table (after KOOLMAN)

Variety tested	Biological strain of Coll. Lind.			
	I	II	III	IV
Red Kidney . . .	S	S	S	R
Red Indian . . . .	S	R	R	S
Navy type . . . .	R	R	S	S
Zebra . . . . .	R	R	R	S

R = resistant  
S = susceptible

As to the degree of immunity it should be remarked that not simply between immunity and susceptibility can be distinguished. There apparently is an almost gradual series of degrees of susceptibility and this makes a genetical analysis very difficult.

v. TSCHERMAK (127, 1919) reports dominance of susceptibility. Other investigators however (McROSTIE 67, 1919 and BURKHOLDER, 5, 1918, 6, 1923) observed dominance of resistance and apparently simple 3 : 1 segregation. The results obtained by TEN DOORNKAAT KOOLMAN in most cases seem to corroborate the latter opinion. Yet the cross of two susceptible varieties gave in  $F_2$  a majority of resistant plants. Also in other crosses unexpected results occur, that at least point to the extremely difficult determination of degree of susceptibility or to more complicate hereditary relations. As a matter of fact the author rightly concludes "dass die Vererbungsverhältnisse doch wohl nicht so einfach liegen, wie es scheinen möchte". This is, in my opinion quite rational. The assumption of special genes for immunity leads to absurd consequences (cf. GÄUMANN 34, 1928). It seems much more probable that a large number of genotypes, without having a special gene in common, are more or less resistant or susceptible, as the case may be. This might fall in line with the opinion of HAMMAR-LUND who considers the transgressive variation with respect to susceptibility in  $F_2$  generations, also observed by BREDEMANN and TEN DOORNKAAT-KOOLMAN, to be due to polymeric factors. According to the latter authors (6, 1927), *Ph. multiflorus* is immune against *Colletotrichum Lindemuthianum*.

TEN DOORNKAAT-KOOLMAN (18, 1927) considers it to be practically immune under normal conditions. When infected under conditions abnormally favourable for infection, some plants may be more or less seriously affected. IVANOV (43, 1928) however says that the new world species (comprising *Ph. vulgaris*, *lunatus*, *multiflorus*, *acutifolius* and *Caracalla*) are susceptible to this fungus, the Asiatic species (*Ph. aureus*, *Mungo*, *aconitifolius*, *calcaratus* and *angularis*) are immune against it, but susceptible to *Cercospora Gruenta*.

Considering *Ph. multiflorus* to be practically immune BREDEMANN and TEN DOORNKAAT-KOOLMAN tried to breed immune races by intercrossing a susceptible *vulgaris*-race with the Scarlet Runner bean. In  $F_3$  and  $F_4$  generations, infected with a mixture of fungus strains, they found a much less pronounced transgression of immune

to susceptible plants than in crosses within *Ph. vulgaris*. The relatively high immunity of *multiflorus* reappears in the offspring and is not correlated with the development of *multiflorus*-like or *vulgaris*-like types. Thus it might be possible to breed in such a way a valuable pantabiotype-immune race of *Ph. vulgaris* habit, in which however they did not succeed as unfavourable characters of the extracted types outweighed this advantage.

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Note after correction: In a recent paper TJEBBES (Hereditas 15, 1931, p. 185—193: Two linkage groups in the garden bean) reports on a close linkage between the factors B (chromogenous factor, that causes mottling when in a heterozygous condition), R (for red colour) and S (for striping of seed coat); crossing-over is less than 1 %. The other linkage group is that of C (also a chromogenous factor) and G (one of a series of triple allelomorphs: Gr, causing green pods and foliage; G, yellow pods and green foliage; g, yellow pods and foliage). Here the crossing-over percentage calculated is about 35 %.

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